Chapter 9

Lumbricidae

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I. INTRODUCTION

The Lumbricidae is the characteristic Oligochaete family of the Palaearctic region. It comprises about 220 species and is a recent and dominant group possessing great powers of adaptation to new surroundings. About 19 species are common over the greater part of Europe and have been carried by man to many parts of the world, where they have locally replaced the indigenous earthworm fauna. In soils where they flourish they dominate the invertebrate biomass and, because of their large size, their effect on the gross physical structure of their habitat is unique amongst the mesofauna.

As a classroom type of the Annelida, "the earthworm" is familiar to every

biology student. Its basic biology is described in standard textbooks and is not repeated here. As classical subjects for laboratory experiment the lumbricids have an extensive literature which was surveyed by J. L. Stephenson in his monograph *The Oligochaeta*, published in 1930. M. S. Laverack's *The Physiology of Earthworms* (1963) provides a critical survey of more recent work in the light of modern physiological concepts and a recent key to the British Lumbricidae is available in Gerard (1964).

II. GENERAL BIOLOGY

Although water is the main constituent of earthworms—about 80–90% of their fresh weight (Grant, 1955a)—the ability to withstand desiccation is one of the most remarkable features of their biology. *Lumbricus terrestris* can survive losing 70% of the water content of its body, and *Allolobophora chlorotica*, 75% (Roots, 1956), and many species can withstand several months of drought in a quiescent state. Nevertheless, although the Lumbricidae are remarkably successful as a terrestrial group, they have a basically aquatic organization.

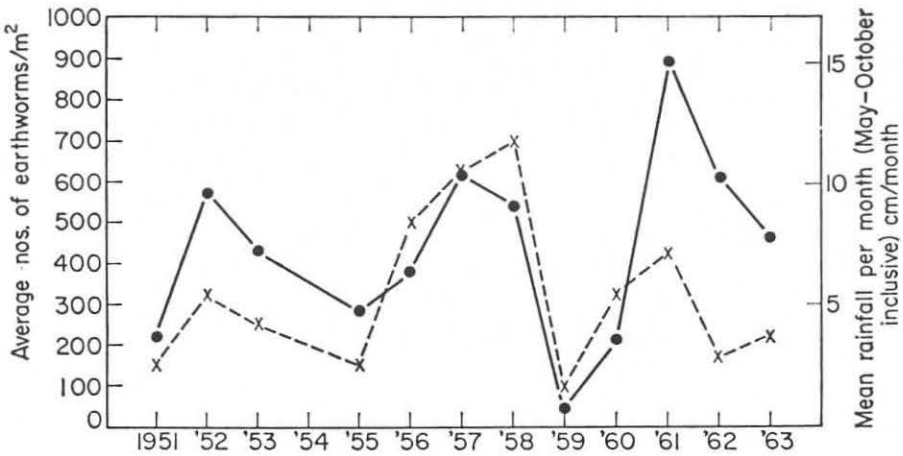

FIG. 1. Earthworm population density and summer rainfall in a Welsh pasture (Reynoldson, unpublished work).

Allolobophora caliginosa, *A. chlorotica* and *A. rosea* comprised 90% of the population. -x—x-, rainfall (cm/month); —●—●—, numbers of earthworms/m².

They lack special respiratory organs and so must maintain a constantly moist body surface for gaseous exchange. Their main nitrogenous excretion is ammonia, which needs a copious hypotonic urine for its elimination. Locomotion and burrowing depend on the hydrostatic pressure of the coelomic fluid and cannot proceed normally if the water content of the body falls by more than 18% (Wolf, 1940). Consequently, the avoidance of desiccation is a keystone in earthworm ecology (Fig. 1).

Evidence will be given later to suggest that competition for food amongst earthworms is often intense and that most of what is known of lumbricid

behaviour and distribution may be interpreted in terms of these two basic requirements, water and food.

Except for species with specialized sub-aquatic habitats, the Lumbricidae fall into two main groups, those like *Dendrobaena octaedra* and *Bimastos eiseni* that live in surface organic horizons and ingest little mineral material, and those like *Octolasium cyaneum* and *Allolobophora caliginosa* that live predominantly in the mineral soil. The division is not absolute, for example *L. terrestris* feeds on plant remains drawn from the surface into its burrow and it also ingests soil; *L. rubellus* lives like *L. terrestris* in mull soils but in soils with raw humus is found only in the organic layers. Nevertheless, there are distinctive differences between the two groups of species. In surface feeding species the body wall is deeply coloured with reddish pigments, identified from *L. terrestris* as protoporphyrin and protoporphyrin methyl ester (Laverack, 1960). Subterranean species lack this pigmentation and are predominantly pale in colour. Except for *L. terrestris*, which remains partly in its burrow while feeding, the surface feeders wander over the ground surface*, whereas subterranean species (Table I) rarely do so, and only when sexually mature.

TABLE

The proportions of pigmented and unpigmented Lumbricidae found in soil samples from limestone grassland and collected on the surface at night (from Svendsen, 1957a)

	Pigmented species	Unpigmented species
Soil samples	168	221
Free on the surface at night	103	25

The pigmentation has been supposed to protect the surface active species from damage by ultra-violet irradiation (Merker and Braunig, 1927) but Kalmus, Satchell and Bowen (1955) found that the unpigmented form of *Allolobophora chlorotica* was unaffected by ultra-violet irradiation several times greater than occurs in daylight. Moreover, *L. terrestris*, which is pigmented, is crepuscular and nocturnal and so is unlikely to need protection

* This occurs during and after rainfall under appropriate temperature conditions and has been reported (Svendsen, 1957a) to take place in Pennine moorland equally in daylight and darkness. This seems inconsistent with what is known of the response to light of *L. terrestris*, which is photonegative to strong light and photopositive to light intensities below about 0·0018 metre candles (Hess, 1924) resulting in the restriction of surface feeding to the hours of dusk and darkness. However, unpigmented species, particularly *O. cyaneum*, which are strongly photonegative to all but the weakest light, are frequently seen in daylight on the surface after heavy rain. Some authors (Merker and Braunig, 1927; Merker, 1928; Nagano, 1934) have regarded this as a response to oxygen deficiency in the soil water, but Roots (1955) considered that water-avoiding reaction alone would explain the worms' behaviour after heavy rain.

from ultra-violet irradiation. The close tonal match between the dorsal surface of pigmented earthworms and soil and dead leaves suggests that pigmentation may be a cryptic adaptation to predation by birds (cf. Southern, 1954). There is experimental evidence that the green pigmented form of *A. chlorotica* survives better than the unpigmented form when subjected to bird predation (Satchell, unpublished work).

A. Reproduction and Life History

Reproduction: Reproduction in the Lumbricidae varies from strict cross breeding in most British *Allolobophora* and *Lumbricus* species to facultative parthenogenesis in *Dendrobaena* and obligate parthenogenesis in *Octolasium*, *Eiseniella*, *Allolobophora rosea* and *Dendrobaena rubida* f. *tenuis* (Muldal,

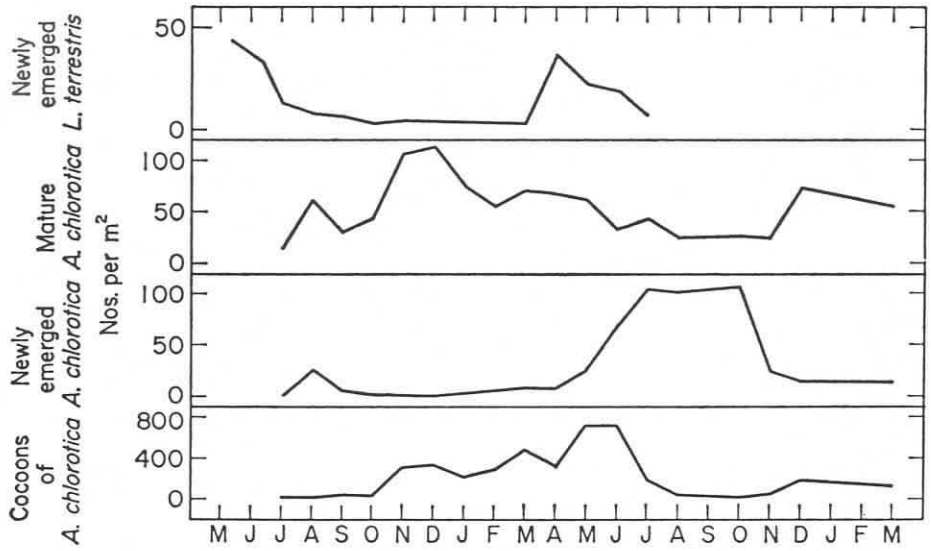

Fig. 2. Seasonal abundance of *A. chlorotica* in "Pastures," Rothamsted 1958–60 (from Gerard, 1960) and of newly-emerged *L. terrestris* in Heaning Wood, Lancs., 1962–63.

1950). *L. terrestris* mates on the surface; other species mate below ground. So far as is known, mating occurs throughout the year except when soil conditions are unsuitable (see pp. 269–271) or the worms are in diapause.

Similarly, cocoon production occurs throughout the year when conditions are suitable. For example, Fig. 2 shows that the number of *A. chlorotica* cocoons in the soil increases from late summer until May–June, when they hatch faster than they are produced.

In many situations, particularly at the limits of their range, earthworm populations may be prevented by adverse moisture and temperature conditions from exploiting the available food resources fully. In less rigorous habitats competition for food appears to be normal. The fecundity of earthworms depends greatly on the food supply (see p. 280), and this homeostatic mechanism regulates the abundance of competing populations. A population

that is greatly decreased, e.g. by prolonged drought (see 1959 data in Fig. 1), may take up to 2 years to recover when conditions are favourable, but usually the reproductive potential is sufficient for populations to adjust rapidly to improved conditions. Table II shows the differing fecundity of

TABLE II

Number of cocoons produced per worm per annum in laboratory cultures (Evans and Guild, 1948)

Species	Year	
	1945	1946
L. rubellus	106	79
L. castaneus	65	—
D. subrubicunda	—	42
D. mammalis	17	—
A. caliginosa	27	27
A. chlorotica	27	25
A. nocturna	3	—
A. longa	8	—
A. rosea	—	8
E. foetida	—	11
O. cyaneum	—	13

lumbricid species kept in laboratory cultures, and although the data may bear little relation to fecundity in the field, there is a striking relationship between the numbers of cocoons produced by the different species and the severity of the environmental hazards they are likely to encounter in nature. For example, the deepest burrowing species (Fig. 3), *A. nocturna*, *A. longa* and *O. cyaneum*, which are most protected from desiccation, produced 3 to 13 cocoons in a year (Evans and Guild, 1948); *L. terrestris*, which also burrows deeply, produces a similar number of cocoons per annum. *A. caliginosa* and *A. chlorotica*, which inhabit the top-soil, produced 25 to 27 cocoons per annum; and *L. rubellus*, *L. castaneus* and *D. subrubicunda*, which live at the soil surface and are most exposed to heat, drought and predation, produced 42 to 106 cocoons in a year.

Moreover, fecundity depends greatly on soil humidity and temperature (Figs. 20 and 23), as does the incubation period of the cocoons. Cocoons of *A. chlorotica* hatch under favourable moisture conditions in about 36 days at 20, 49 days at 15 and 112 days at 10° C (Gerard, 1960). For some species the range in incubation period is extremely large (Fig. 4). For example, Evans and Guild (1948) record that batches of *A. caliginosa* and *L. castaneus* cocoons, all laid within a fortnight, hatched in two distinct groups separated by 10 to 12 weeks of low winter temperatures. The physiology of incubation is not understood, but a flexible incubation period that enables a species to survive adverse seasons is clearly an advantage. Normally the factors that

control cocoon production and incubation period in *L. terrestris*, *L. castaneus* and *A. chlorotica*, and probably other species, synchronize to produce pronounced peaks of emergence in the spring and early summer (Fig. 2), when the growth rate may be 3 to 4 times greater than at other times of the year (Satchell and Skellam, unpublished work).

Like incubation, the growth period from emergence to sexual maturity is flexible and depends on environmental conditions (Table III and Fig. 5). For example, the periods recorded for *A. chlorotica* are 13 weeks at 18° C (Michon, 1954), 17 to 19 weeks at 15° C (Graff, 1953) and 29 to 42 weeks in an

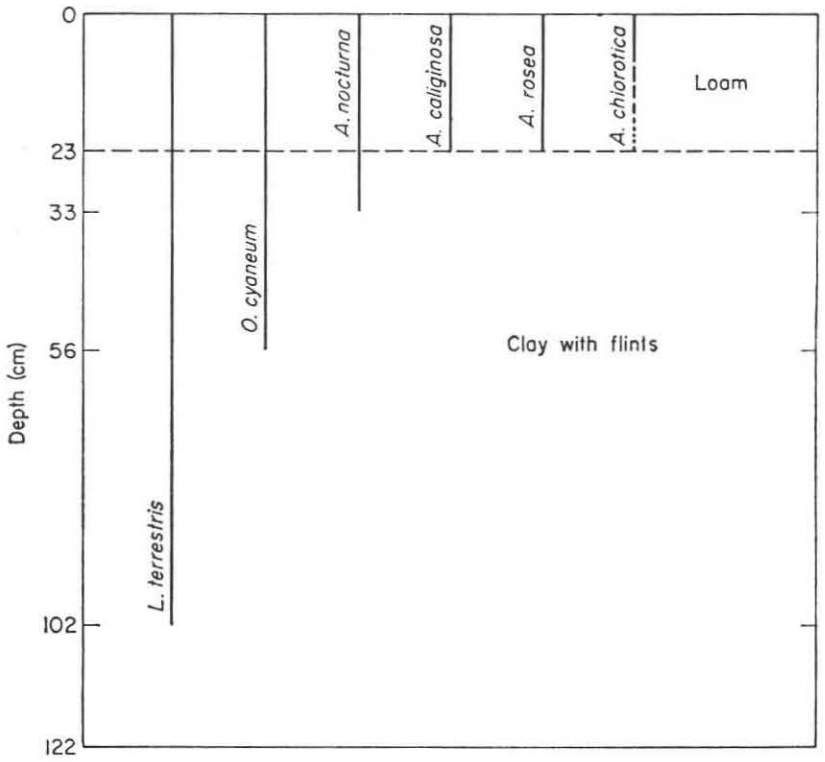

FIG. 3. Vertical distribution of earthworms in a Rothamsted pasture (from Satchell, 1953).

unheated cellar (Evans and Guild, 1948). In woodlands near Merlewood Research Station, Lancashire, there is a peak emergence of this species in early summer, and the population contains the greatest proportion of adults

TABLE III

Growth period (days) from emergence to sexual maturity of *Eisenia foetida* kept at constant temperature (Michon, 1954)

Food	28° C	18° C
Dung	46	59
Tilia leaves	62	91

in the winter following. Development to sexual maturity therefore appears to take about 6 months. *L. terrestris* matures in these sites in about 1 year.

The breeding life of most lumbricids is probably quite short, rarely more than a few months, and much interrupted by unfavourable conditions (see

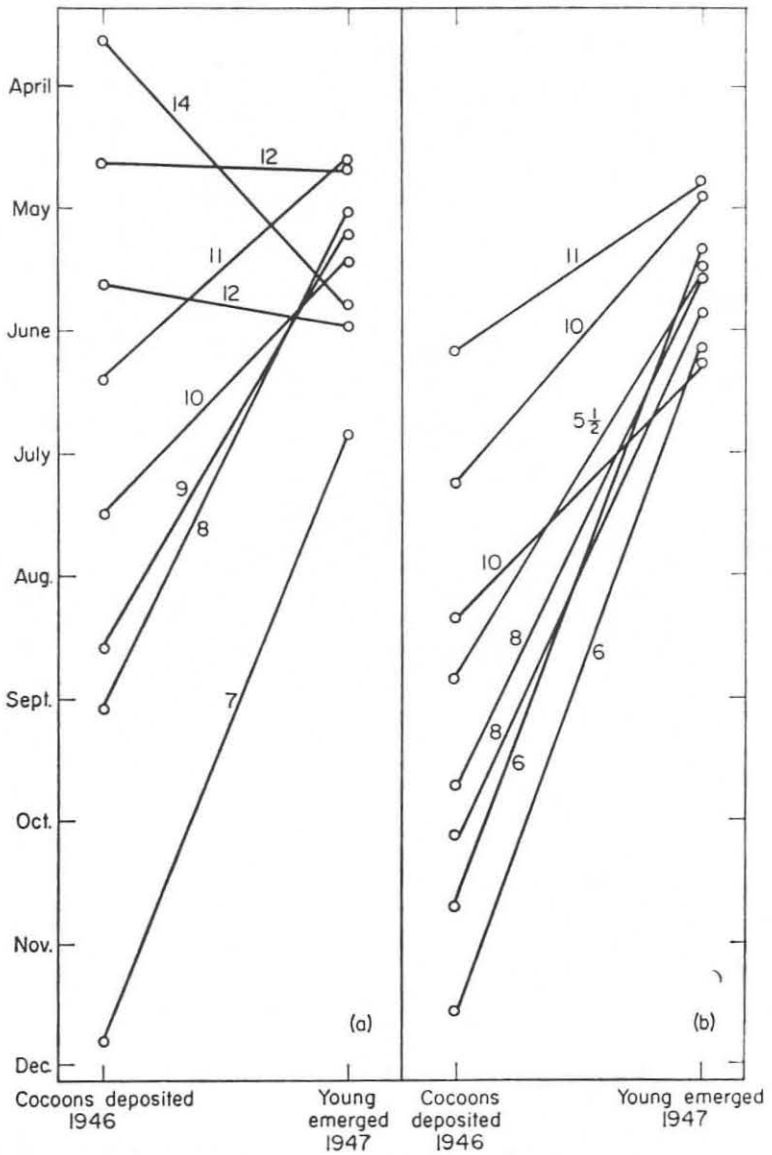

FIG. 4. Incubation periods of cocoons (adapted from Evans and Guild, 1948). –o$\overset{6}{\text{——}}$o–, incubation time in months. (a) *L. castaneus*; (b) *A. caliginosa*.

p. 266). In the laboratory, individual specimens of *E. foetida*, *L. terrestris* and *A. longa* have been kept for $4\frac{1}{2}$, 6 and $10\frac{1}{4}$ years respectively (Korschelt, 1914), but these represent the ends of very skew longevity distributions. An average life of rather less than 2 years has been recorded for 10 common field species kept at 18°C, ranging from 15 months for *A. chlorotica* to 31 months

for *A. longa* (Michon, 1954). The phenology of maturation, reproduction and senescence observed in these cultures (Fig. 5) differed from that of *L. terrestris* in cultures kept in the ground outdoors (Satchell, 1963) (Fig. 6). These worms became sexually mature at about 1 year, and about half survived at least 3

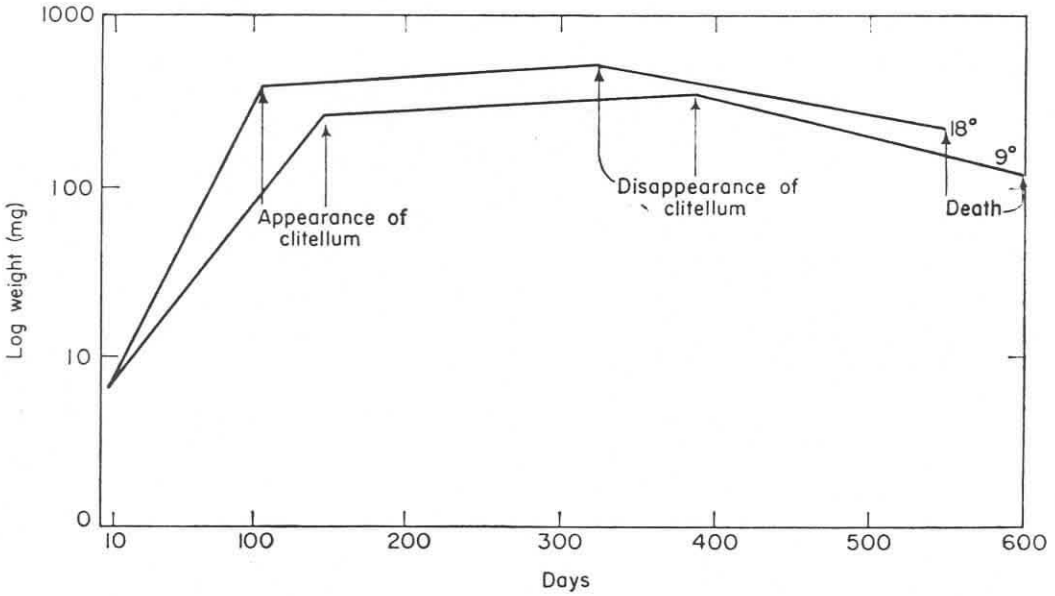

FIG. 5. Development of *Dendrobaena subrubicunda* at 18 and 9°C (from Michon, 1954).

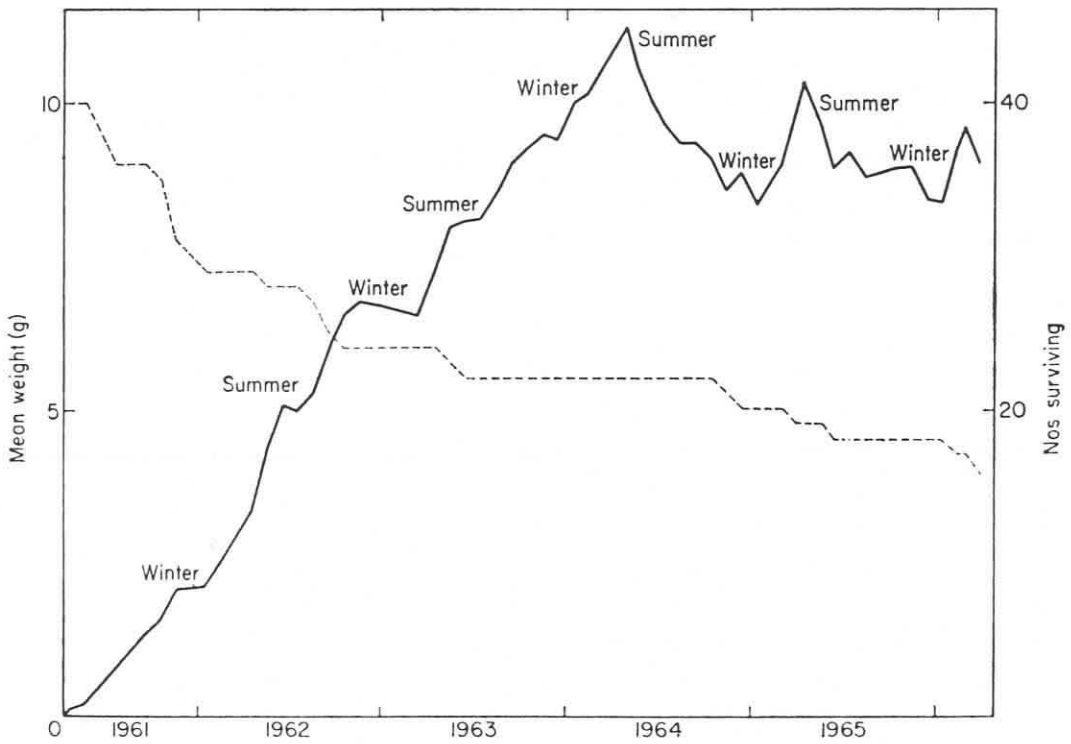

FIG. 6. Growth increment and mortality (·····) of *L. terrestris* reared outdoors.

years showing no sign of senescence. The mortality rate was approximately constant throughout, individuals losing weight before death. The causes of death are unknown, but some individuals which lost weight contained hyphae of a phycomycete in a dense web surrounding the intestine. Growth rate studies and size class frequencies in field populations suggest that the average life of this species is about 15 months, although a few individuals may survive for 8 or 9 years.

B. Seasonal Activity in Relation to Soil Moisture, Temperature and Food Resources

Earthworm activity in the field is markedly seasonal. The production of faeces in the form of wormcasts on the soil surface shows marked maxima in spring and autumn and may cease completely at other times of the year (Fig. 7). Similarly, the numbers of earthworms collected by vermifuge

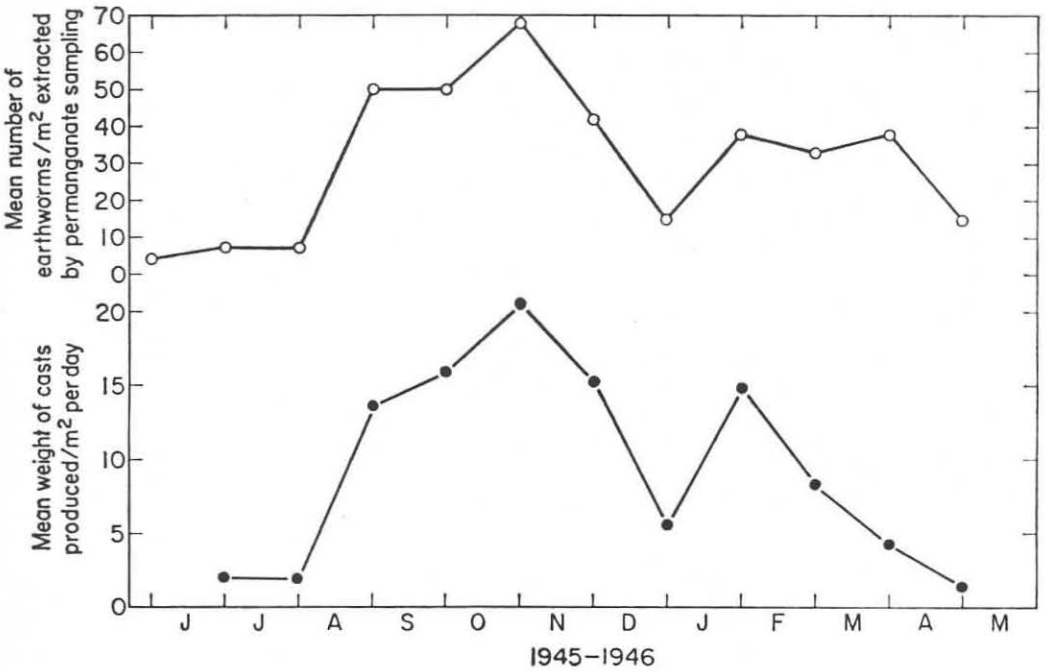

Fig. 7. Seasonal variation in worm cast production and numbers of earthworms extracted by permanganate sampling, Great Field, Rothamsted (redrawn from Evans and Guild, 1947).

sampling, which depends on the activity of the worms to bring them to the soil surface, tend to show spring and autumn maxima (Fig. 7). In both these examples activity has been shown to be correlated with soil temperature and soil moisture (Evans and Guild, 1947), but the response to these factors varies considerably between species.

1. Seasonal activity in L. terrestris

For *L. terrestris*, the relationship between activity and soil temperature can be represented approximately by the curve shown in Fig. 8. This is derived from the numbers of worms collected from woodland sites near Merlewood by a standardized sampling procedure using dilute formaldehyde as an expellant. It is based on a large number of samples taken over a period of 2

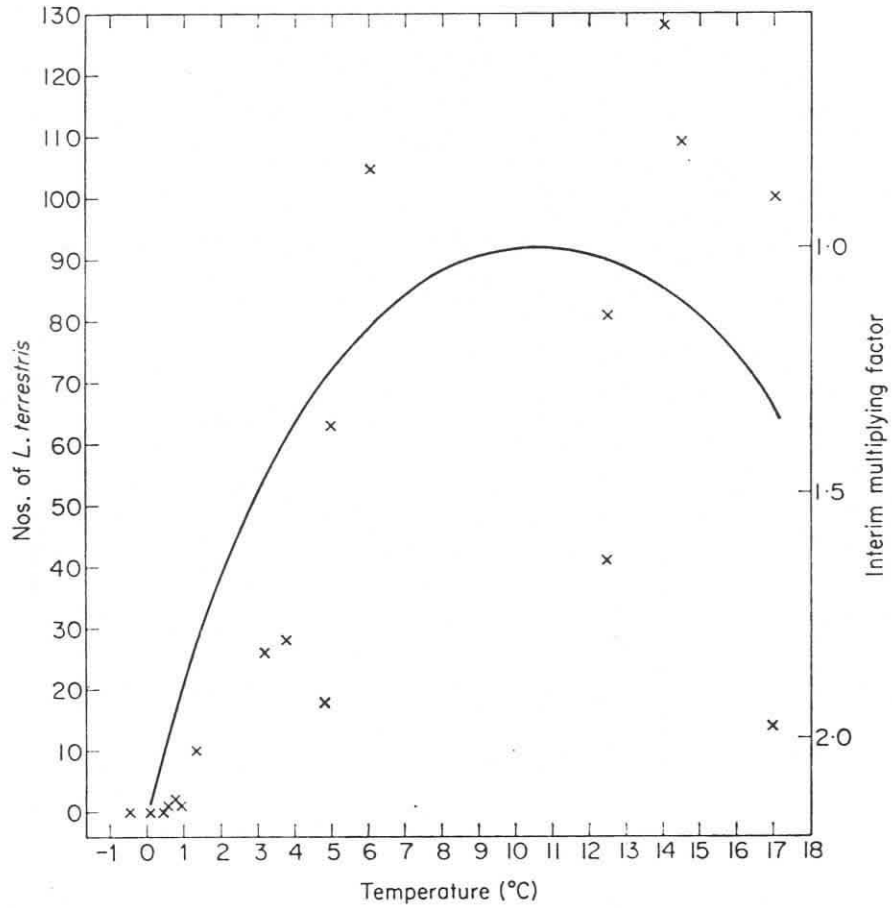

FIG. 8. Motor activity of *L. terrestris* in relation to temperature. ×, numbers of *L. terrestris* on the surface of a garden plot 17 m² (data from Kollmansperger, 1955). Curve indicates temperature correction factor for estimating *L. terrestris* biomass from weights of worms expelled by formaldehyde (see text).

years, and is corrected for variations in population density. The optimum soil temperature (at a depth of 10 cm) for response to the expellant appears to be about 10·5° C.

The numbers of worms found on the soil surface at night can also be used as an index of activity, provided population density is constant. In Fig. 8 the numbers of worms active on the surface of a garden plot in Germany and the prevailing ground temperatures are shown (Kollmannsperger, 1955), with the formaldehyde sampling temperature curve superimposed. The data,

which are selected to include only nights after recent rain, are consistent with the curve and suggest an optimum temperature of about 10·5° C for surface activity. Figure 9 shows similar data for earthworms active on a close mown lawn at Merlewood.* They represent the worms, mainly *L. terrestris*, seen on a permanently marked-out area of 12 m² during counts begun at 1 a.m. on 40 nights in March–May 1962. The records suggest that the nights most

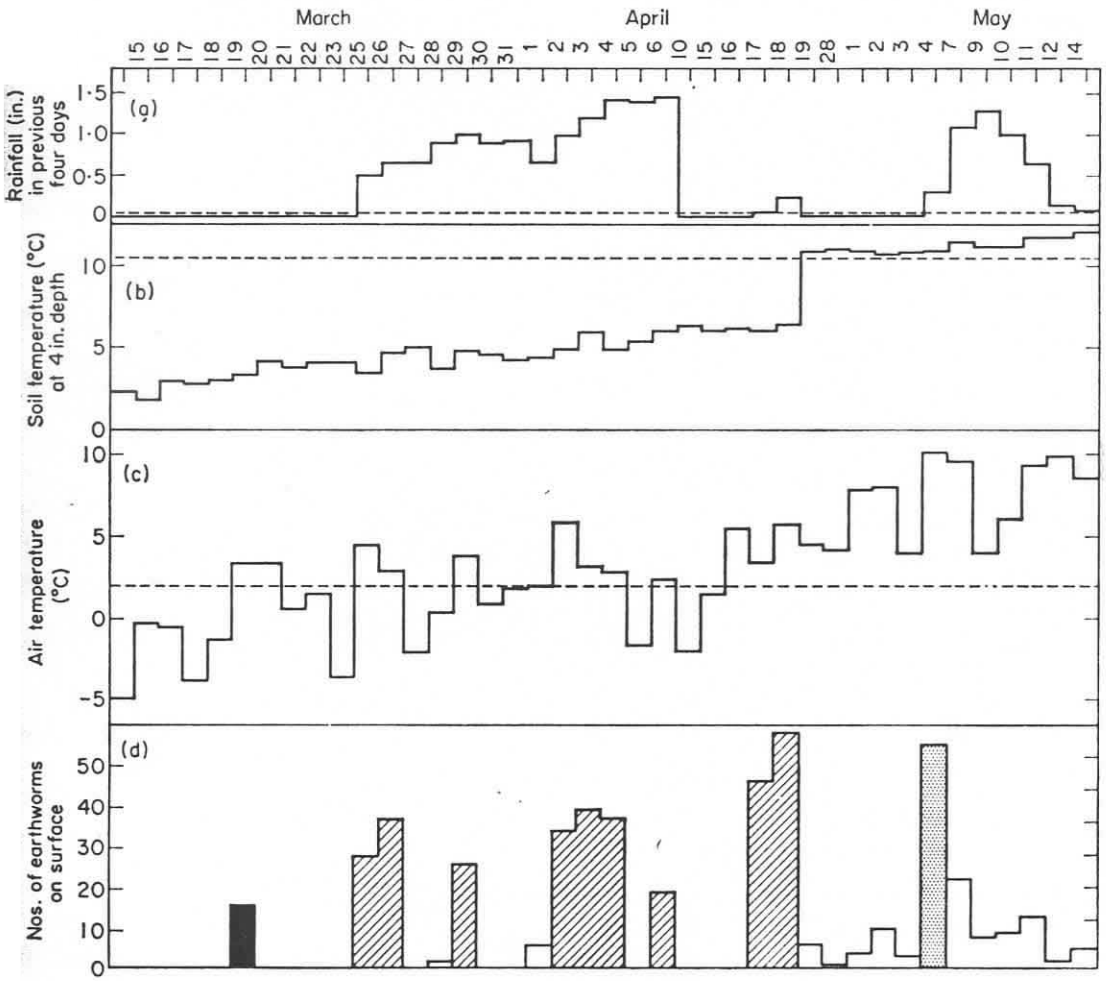

FIG. 9. Surface activity of *L. terrestris* in relation to rainfall and temperature.
(a) Rainfall (in) in previous four days; (b) soil temperature (°C) at 4 in depth; (c) air temperature (°C); (d) numbers of earthworms on surface: ■, temperature rise after 7 nights below zero; ▨, air temperature above 2° C, soil temperature below 10·5° C, rainfall during previous 4 days; ▩, rainfall following 12 rainless days.

suitable for earthworm activity were those when grass air-temperatures were above 2° C, when soil temperatures did not exceed 10·5° C and when there had been some rain within the previous 4 days. All the main peaks of activity occurred in such conditions except two, and both of those followed long periods of inactivity. If it is sufficiently hungry, *L. terrestris* will apparently come out to feed when it would not otherwise be active on the surface. The

* Recorded by J. M. Nelson.

number of leaves buried by *L. terrestris* kept at constant temperature (Table IV) also suggests that the optimum temperature for motor activity is near 10° C. This is about 2·5° C less than the optimum found by Laverack (1961a) (Fig. 10) for segmental nerve preparations for *L. terrestris*, but the difference may be accounted for by cerebral or synaptic inhibition of motor response.

TABLE IV

Number of leaves buried by 20 *L. terrestris* in 4 months at constant temperatures (Raw, unpublished data)

Temperature (° C)	0	5	10	15
No. of leaves buried	0	178	204	174

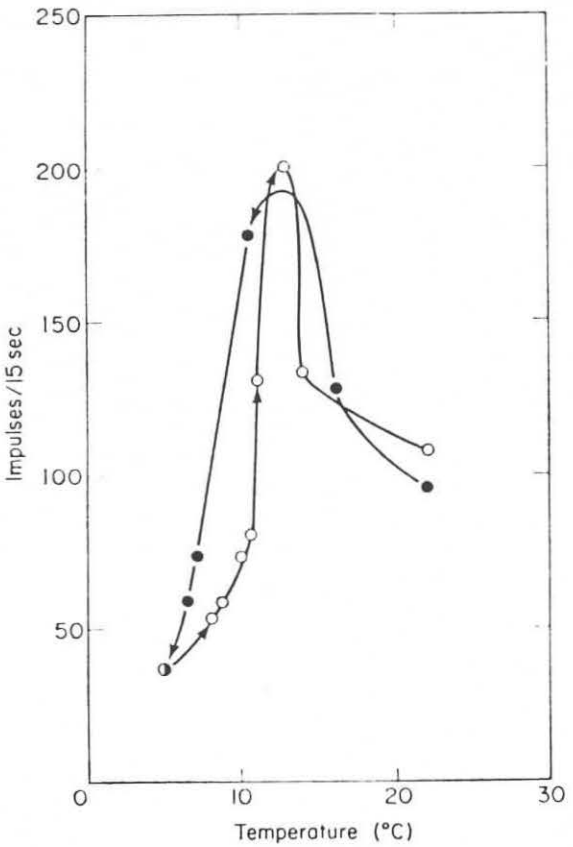

FIG. 10. Graph showing steady rate curve of nervous activity for a range of temperatures. The number of impulses rises towards an optimum at 13° C and then falls as the temperature increases further (from Laverack, 1961a).

The surprisingly low level of the optimum temperature for activity raises questions as to its ecological significance. It can be of no importance as a protection against heat death because the upper lethal temperature for *L. terrestris*, 28° C (Wolf, 1938a), is unlikely to be encountered by earthworms in nature. The negative phototaxis of *L. terrestris* restricts it to crepuscular and nocturnal surface activity, and its deep burrows protect it from the hazards

of desiccation in the topsoil, encountered by many species. Moreover, earthworms move away from drying air irrespective of the temperature (Parker and Parshley, 1911; Wolf, 1938b).

Except in very cold weather and during nocturnal surface activity, *L. terrestris* generally occupies the topsoil where, in temperate forests, the temperature rarely exceeds 10·5° C except between mid-May and October (Fig. 32). At this season food supplies from one leaf fall have virtually ended and have not yet been replenished from the next (see Fig. 29). If the respiration rate of *L. terrestris* increased with increasing temperature during this period, death by starvation could follow. The basal metabolic rate of *L. terrestris* increases with rising temperature almost to the thermal death point (Pomerat and Zarrow, 1936), but the reduction of motor activity at temperatures above 10·5° C may counteract this (see pp. 268) and could actually decrease metabolism. The control of motor activity by ambient temperature can thus be regarded as an indirect mechanism that limits oxidative metabolism at a time when food is scarce.

2. *Seasonal activity in* Allolobophora *spp.*

The activity of sexually mature *Allolobophora longa* and *A. nocturna* is interrupted by summer diapause. In nature this begins in May, when soil temperatures are rising and soil moisture is falling. The worm stops feeding, lines a small cell with mucus, rolls into a ball and enters an inactive state during which it loses its secondary sexual characters. It cannot be aroused by changes in soil temperature or humidity, but diapause ends spontaneously in late September or October. Michon (1954) found that diapause did not occur in worms reared at about 9° C with adequate food and soil moisture but more recent work (Doeksen and van Wingerden, 1964) has not confirmed this.

Diapause contrasts with the quiescent state which occurs in immature specimens and also in *A. chlorotica*, *A. caliginosa* and *A. rosea* (Evans and Guild, 1947), when the worms roll up into a ball as the soil becomes too cold or too dry (Table V) and become active again immediately soil conditions become favourable. The ecological significance of this difference is not understood. There is considerable disagreement in the reports of various authors

TABLE V

Percentage of *Allolobophora* spp. in aestivation in an irrigated and a covered plot. Rothamsted 1959–60 (Adapted from Gerard, 1960)

% Aestivating	July	Aug.	Nov.	Feb.	May
Irrigated plot	3·8	0	0	0	6·3
Covered plot	100	100	28·5	0	48·1
% Soil Moisture (0–20 cms)					
Irrigated plot	18·2	21·2	23·7	23·6	23·2
Covered plot	11·5	10·2	10·0	18·3	9·4

(Avel, 1929; Evans and Guild, 1947; Michon, 1957; Doeksen and van Wingerden, 1964; Doeksen, 1964) on details of the behaviour of a number of species, and the subject requires further study, particularly of the neurosecretory mechanisms involved.

Fig. 7 shows seasonal changes in wormcast production by *A. longa* and *A. nocturna.*

III. EARTHWORM POPULATIONS— BIOMASS, DISTRIBUTION AND REGULATION

A. Methods of Population Sampling

Of the numerous methods used to sample earthworm populations, none are equally suitable for all species and all habitats. Evans and Guild (1947), in their pioneering studies on the earthworm populations of agricultural soils in Britain, used potassium permanganate solution to expel worms from the soil, a method limited by the penetration of the solution and the variable response of the earthworms to it. Sorting soil samples by hand is a more efficient procedure for soils that can be easily crumbled (Svendsen, 1955b), but most specimens less than 2 cm long are missed (Nelson and Satchell, 1962). For sampling small species, such as *Eiseniella tetraedra,* in wet, matted hill grassland, Raw (1960) used a method of flotation in magnesium sulphate solution which extracted more than twice the number found by hand sorting. Hand sorting is also impracticable for sampling *L. terrestris*, which when disturbed retreats down its burrow a metre or more deep. The discovery of formaldehyde solution as an expellant for this species (Raw, 1959) and the development of a method of biomass estimation which allows for the effect of soil temperature on the proportion of the population expelled (Satchell, 1963), has opened up the study of this important species in soil biology.

B. Biomass

Estimates of earthworm biomass (Table VI) based on formaldehyde sampling, approximately 100 to 250 g/m^2, suggest that the weight of earthworms in mull sites where *L. terrestris* is present is considerably greater than earlier methods indicated. In particular, Bornebusch's (1930) estimate of 61 g/m^2, which is much quoted in comparative studies of energy turnover by soil fauna, is much too low to be typical of woodland mull. Present estimates suggest that the earthworm biomass of grassland and woodland are similar on similar soils. Lower weights are found in arable land, but they can exceed 100 g/m^2 in fields heavily dressed with dung (Raw, 1961a). Estimates of up to 5 g/m^2 for woodland raw humus and acid moorland sites (Table VI) indicate that the earthworm fauna there differs from that of other habitats and lacks the large, deep burrowing species.

All the above figures are subject to large standard errors arising from seasonal and spatial variation. In a mixed population of *A. caliginosa* and

TABLE VI

Numbers and weights of earthworms in various habitats

	No./m²	g/m²	Locality	Sampling method	Authority
Eriophorum moor	0·01		Moor House, Westmorland	Dung baiting	Svendsen (1957b)
Calluna moor	0·1–0·5		Moor House, Westmorland	Dung baiting	Svendsen (1957b)
Picea raw humus (2 sites)	18–31	0·9–1·5	Denmark	Tullgren funnels	Bornebusch (1930)
Fagus raw humus (2 sites)	23–81	1·2–5·4	Denmark	Tullgren funnels	Bornebusch (1930)
Pseudotsuga raw humus	14	4·7	Bangor, N. Wales	Hand sorting	Reynoldson (1955)
Picea mull	101	5·1	Denmark	Tullgren funnels and hand sorting	Bornebusch (1930)
Fagus mull (3 sites)	73–177	5·9–54	Denmark	Tullgren funnels and hand sorting	Bornebusch (1930)
Quercus mull	122	61	Denmark	Tullgren funnels and hand sorting	Bornebusch (1930)
Mixed wood mull	157	40	Bangor, N. Wales	Hand sorting	Reynoldson (1955)
Mixed wood mull (2 sites)	78–493	148–162*	Lake District	Formaldehyde	Satchell (unpublished)
Apple orchards under grass	25–500	11–122	Holland	Hand sorting	Van Rhee and Nathans
(23 plots)	848	287	Wisbech, Cambs.	Hand sorting and formaldehyde	Raw (1959) [(1961)
Apple orchards under arable	13–30	11–23	Holland	Hand sorting	Van Rhee and Nathans
cultivation (4 plots)	196	153	Wisbech, Cambs.	Hand sorting and formaldehyde	Raw (1959) [(1961)
Arable land	220	48	Germany	Wet sieving	Krüger (1952)
Arable land	287	76	Bardsey Island	Hand sorting	Reynoldson *et al.* (1955)
Arable land	146	50	Bangor, N. Wales	Hand sorting	Reynoldson (1955)
Arable land (4 sets of plots)		50–106	Rothamsted	Formaldehyde	Raw (1961a)
Base rich grassland (2 sites)	389–470	52–110†	Moor House, Westmorland	Hand sorting	Svendsen (1957b)
Base rich grassland (2 sites)	390	56	Bardsey Island	Hand sorting	Reynoldson *et al.* (1955)
Base rich grassland (2 sites)	481–524	112–120	Bangor, N. Wales	Hand sorting	Reynoldson (1955)

* Yearly averages corrected for temperature variation.

† *L. terrestris* is uncommon on these sites. Only 1 m² was sampled for each estimate.

L. rubellus in a New Zealand pasture the weight of earthworms found by Waters (1955) varied, during 2½ years monthly sampling, between approximately 140 g/m² in the summer to about 269 to 324 g/m² in the winter (Fig. 11). A similar seasonal fluctuation in the biomass of *L. terrestris* occurred in woodland mulls near Merlewood (Fig. 11).

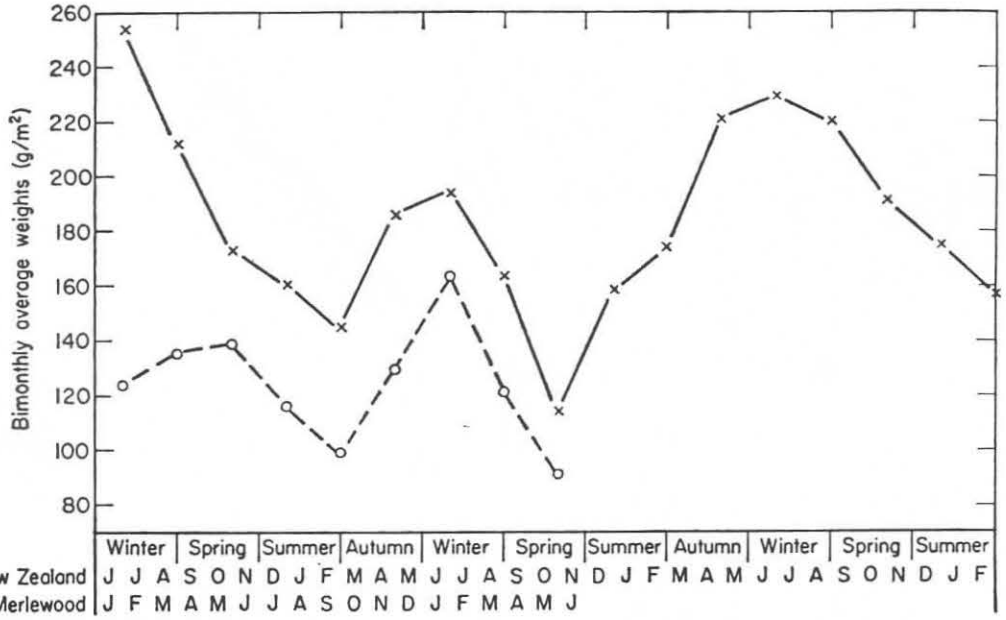
Bimonthly average weights (g/m²)
260
240
220
200
180
160
140
120
100
80
Winter | Spring | Summer | Autumn | Winter | Spring | Summer | Autumn | Winter | Spring | Summer
New Zealand J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F
Merlewood J F M A M J J A S O N D J F M A M J

FIG. 11. Seasonal variation of earthworm biomass. –x–x–, *A. caliginosa* (1951–54, New Zealand; from Waters, 1955); –o—o–, *L. terrestris* (1960–61, Merlewood; Satchell, unpublished work).

C. POPULATION AGGREGATION

On one of these sites near Merlewood 10 quadrats, each 0·5 m², were sampled by the formaldehyde method on each of 31 occasions. On one occasion the biomass of *L. terrestris* in individual quadrats ranged from 24 to 113 g. The standard error for the 10 samples varied on the 31 occasions between 6 and 17% of the mean.

The very patchy distribution which these figures reflect is typical of earthworm distribution generally. It is common amongst such species as *L. castaneus* (Fig. 12) which roam over the ground surface and aggregate under dung or similar localized food sources. It also occurs, however, where there is no particular concentration of food as a result of localized concentrations of cocoons. *L. terrestris*, for example, deposits its cocoons in the topsoil near the mouth of its burrow so that a "family" group is formed when the cocoons hatch in the spring. In species such as *L. castaneus*, with a marked seasonal abundance, the spatial distribution passes from a highly aggregated phase in the early summer when the population consists mainly of immature worms, through an intermediate phase when the aggregation is weakened by dispersal and mortality to a winter phase when the population is low, predominantly adult and randomly distributed (Satchell, 1955).

D. Species Distribution and Density Regulation

Unless saline or very deficient in organic matter, few soils in the temperate zone are incapable of supporting some species of earthworm. Barley (1961) expresses this in the working rule that where temperate grasses can grow, some species of earthworm can also grow. Many factors affect their distribution, the physical and chemical characteristics of the soil, the type of vegetation, and land management, but in most soils the primary factors that determine the population are the supplies of available water and food.

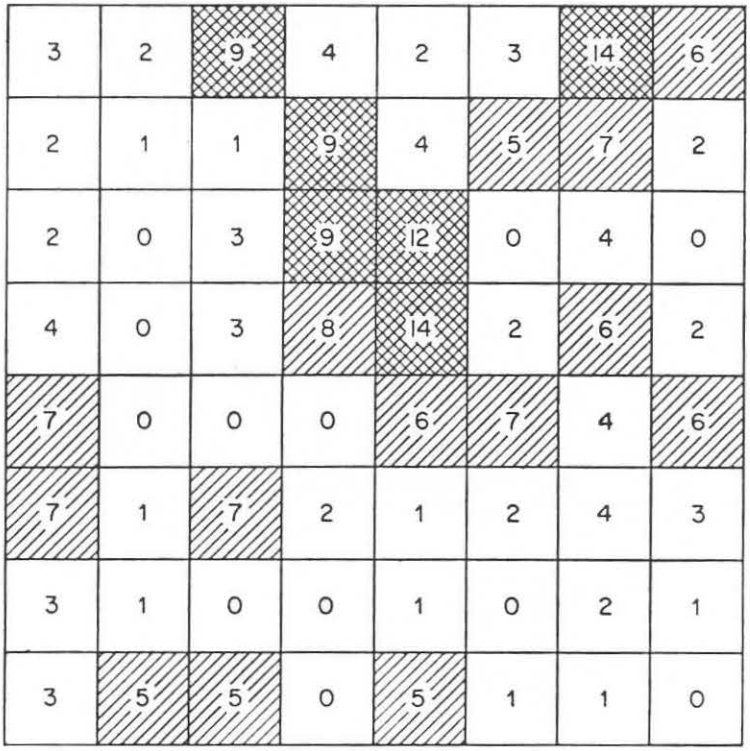

FIG. 12. Distribution of *L. castaneus* in a quadrat 8 × 8 yd (approx. 53·5 m²). ▩, more than 8 *L. castaneus*/yd²; ▨, 5–8 *L. castaneus*/yd²; □, less than 5 *L. castaneus*/yd².

1. Distribution in mull and mor

Table VII shows the distribution of some common earthworm species collected from some Lake District woodlands by hand sorting. The five mull sites are on base rich soils overlying carboniferous limestone, the sites with mor humus, which is of a moder type, overlie base poor slates and shales of the Bannisdale series. Table VIII, taken from Guild (1948), shows the earthworm distribution in a similarly contrasting pair of sites under rich pasture and moorland herbage. In the mull sites, about 8 characteristic species are found, of which three, *L. terrestris*, *A. longa*, *O. cyaneum*, are large worms several grams in weight. In the moder or peaty sites, rarely more than 4 species occur, all are less than 1 gram weight and the largest, *L. rubellus*, is much less

TABLE VII

Distribution of Lumbricidae in 10 Lake District woodlands

	Mull sites					Mor sites					Average size of mature field specimens (g fresh wt.)
	Yew		Sycamore			Hazel		Birch	Oak	Spruce	
pH of litter	6·6	7·5	5·9	4·2	6·2	4·5	4·3	4·3	4·1	4·1	
pH at 15 cm	8·0	6·7	6·3	5·4	5·8	3·7	3·7	3·3	4·0	3·9	
A. rosea		×		×	×						0·41
A. longa	×	×		×	×						2·29
A. caliginosa			×	×	×						0·47
A. chlorotica	×	×	×	×	×						0·40
Octolasium cyaneum	×	×	×	×	×		×				1·98
L. castaneus	×	×	×	×	×	×					0·25
L. terrestris	×		×	×	×		×				5·58
L. rubellus	×		×	×	×	×	×	×	×		0·75
D. rubida agg.		×	×		×			×			0·20
D. octaedra						×	×	×	×	×	0·13
Bimastos eiseni						×	×	×	×	×	0·25

TABLE VIII

Species composition of two earthworm populations sampled by the permanganate method (from Guild, 1948)

Species	Good quality pasture with much clover (No./m²)	Acid peaty soil with coarse herbage and heather (No./m²)
A. longa	1·2	—
A. chlorotica	0·2	—
A. caliginosa	19·5	—
A. rosea	4·4	—
O. cyaneum	1·4	—
L. terrestris	5·8	0·1
L. castaneus	8·2	0·1
L. rubellus	15·3	5·3
D. rubida	1·3	2·0
D. octaedra	0·1	1·8
B. eiseni	—	3·1

abundant than in mull sites. Under increasingly eutrophic conditions, *L. rubellus* and species of the *D. rubida* complex decrease until only *D. octaedra*, and *B. eiseni* remain (Fig. 13) as the characteristic species of such extreme habitats as *Calluna* heath and conifer mor. It is interesting that although these species are adapted to mor sites and are most abundant there, their total biomass is small despite the abundant energy supplies present in the organic matter. Although it is commonly stressed that a mor fauna contains few

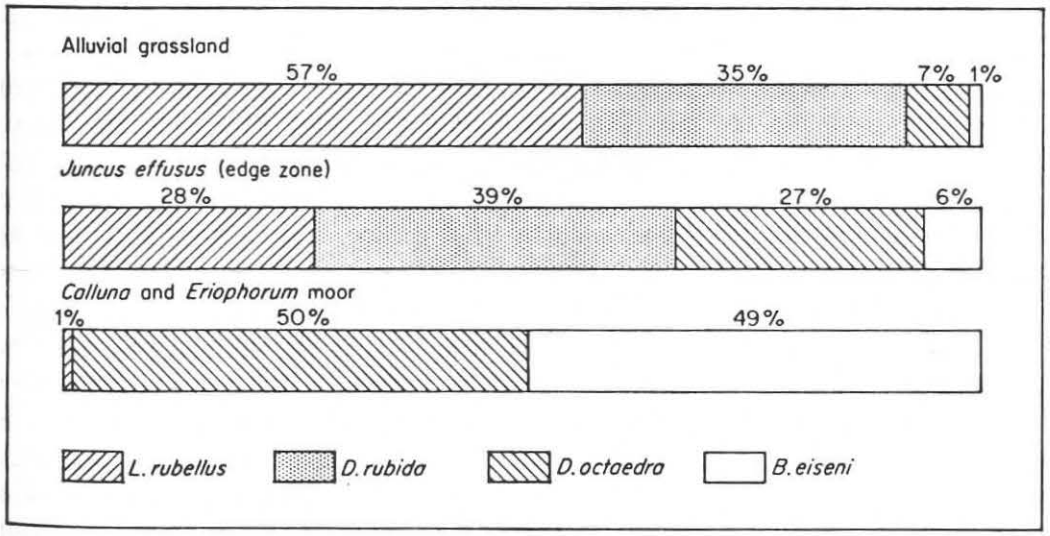

FIG. 13. The relative proportions of 4 species of lumbricids found aggregated in sheep dung on different vegetation types on Moor House National Nature Reserve (from Cragg, 1961).

species, there are many species of enchytraeids, microarthropods, larval Diptera and other groups adapted to mor conditions. The fact that organic horizons persist despite their presence shows that they, and the microflora on which many of them feed, are physiologically unable to fully exploit mor forming litter as food. Handley (1954) suggests that the organic nitrogenous material in mor is less easily digestible than that in mull.

2. Food as a population determinant

(a) *The effect of added food supplies on field populations.* It has already been stated that competition for food is a primary population determinant. One form of evidence for this is the population increase which occurs when food is supplied experimentally in the field. Examples from arable land, grassland and heath are given in Table IX. The first, Broadbalk, is under continuous wheat cropping, and the earthworm population of the plot that receives 14 tons (approx. 35 m. tons/ha) of farmyard manure per acre annually is 3 to 4 times as great as that on an unmanured plot. On Park Grass, a permanent mowing meadow, the earthworm population of a plot receiving 14 tons of farmyard manure and 6 cwt of guano (0·75 m. tons/ha) per acre every fourth year was, in 1952, three times greater than that of an unmanured plot. On Silpho Moor, an acid *Callunetum*, occupied almost solely by *Bimastos eiseni*, 8 years of applying birch litter to the heather at rates simulating natural leaf fall increased the population from less than 1 worm per 20 m^2 to between 1 and 5 worms/m^2.

(b) *Nitrogen as a limiting food constituent.* In the Silpho Moor experiment the nitrogen content of the birch litter was 2 to 3 times that of the *Calluna* litter, and the treated plots on Broadbalk and Park Grass at Rothamsted received heavy dressings of organic nitrogen. The response of the earthworm populations is consistent with much additional evidence that points to the importance of available protein in determining earthworm distribution and abundance.

Barley (1959) and Evans and Guild (1948) have shown that in laboratory cultures earthworms fed on nitrogen rich diets grow more (Table X) and produce more cocoons (Table XI) than worms fed on nitrogen poor diets. Moreover, estimates of the nitrogen requirements of field populations suggest that protein supplies limit earthworm abundance. The amount of nitrogen excreted annually by a population of *L. terrestris* in Merlewood Lodge Wood, a Lake District ash-oak wood, is calculated as being about 33 kg/ha (p. 304). The amount of nitrogen available to this population has not been determined but, by analogy with similar woodlands, the annual production of tree litter is likely to be about 3,000 kg/ha with an average nitrogen content of about 1·5% and that of the ground flora about 8 kg/ha of nitrogen. On this basis the total nitrogen content of the annual litter production from trees and herbage would be about 50 kg/ha, which is about one-third more than the estimate of the amount excreted annually by the *L. terrestris* population.

TABLE IX

Earthworm populations of plots treated with organic materials and control plots (No./m²)

1. Arable
Broadbalk, Rothamsted
(from A. C. Evans, unpublished work)

	Control	Dung
No. (all species)	74·1	271·8
Weight (all species (g/m²)	5·0	50·3

Barnfield, Rothamsted
(from Raw, 1961)

	g/m² (all species)	
Inorganic nitrogen fertilizer	Control	Dung
NH_3SO_4	2·5	106·1
$NaNO_3$ (+rape cake)	24·1	78·8
$NaNO_3$	10·2	62·4
None	3·9	49·5

2. Grassland
Park Grass, Rothamsted
(from Satchell, 1955)

	Control	Dung
A. caliginosa	2·9	8·0
A. nocturna	1·3	18·9
A. chlorotica	1·6	0
A. rosea	10·0	21·3
L. castaneus	16·0	59·6
L. terrestris	13·1	22·5
O. cyaneum	6·9	24·5
Total	51·8	154·8

3. Heather Moor
Silpho Moor, N. Yorkshire
(from Satchell, unpublished work)

	Control	Birch Litter
B. eiseni		
Replicate 1	0	1·4
Replicate 2	0	3·0
Replicate 3	0	5·4
Replicate 4	0	0·6

However, *L. terrestris* ingests, besides litter, a considerable amount of soil. Specimens of various sizes taken from Merlewood Lodge Wood population in March 1961 contained 100 mg of soil (oven dry wt.) per gram body weight. In this species food passes through the gut in about 20 (Parle, 1963b) −24 hours (Satchell, unpublished) so the rate of ingestion appears to be about 100 to 120 mg/g per day. This will of course vary with soil temperature and internal factors affecting the metabolic rate, but if it were maintained for 200 days in a year, the total annual soil intake by the population which had a

TABLE X

Change in body weight of *A. caliginosa* when fed for 40 days on various diets (from Barley, 1959)

	% N content of diet	% Wt. change in worms
Sandy loam soil	0·04	−53
Phalaris tuberosa roots	0·8	−26
Phalaris tuberosa leaves	2·0	−26
Clover roots	2·6	−2
Clover leaves	4·5	+18
Dung on surface	3·3	+71
Dung incorporated		+111

TABLE XI

The cocoon production of two species of earthworms on various types of organic matter (from Evans and Guild, 1948)

	Mean no. of cocoons produced by 5 earthworms in 3 months	
Organic matter	*A. chlorotica*	*L. castaneus*
Fodder	0·8	9·4
Oat straw	1·4	12·0
Bullock droppings	12·4	73·2
Sheep droppings	14·0	76·0

mean biomass of 120 g/m² would be about 2,640 g/m². The nitrogen content of the soil at 10 cm depth in Merlewood Lodge Wood is 0·46% (oven dry wt.), so the amount of nitrogen ingested in soil would be about 121 kg/ha. The total nitrogen available to the population from ingested soil and the entire leaf fall would therefore be about 170 kg/ha. Barley (1959) has shown that of the insoluble nitrogen ingested by *A. caliginosa*, 6·4% is excreted in soluble metabolized forms. If a similar proportion of the ingested organic nitrogen is metabolized by *L. terrestris*, and if the food materials were ingested only

once in one year, then the total nitrogen excreted annually would be about 11 kg/ha, which is only one-third of that estimated from the excretion data referred to on p. 304. It may be that *L. terrestris* digests protein more efficiently than *A. caliginosa*, but even if it were three times as efficient it would still need the whole of the woodland's litter output to balance its nitrogen excretion rate. As there are other competitors for the litter, the demand must be met by selective feeding on some additional richer source of nitrogen. The soil organic matter of a woodland mull (Heaning Wood) similar to that in Merlewood Lodge Wood has a nitrogen content of 4·9% (Howard, personal communication) and although it can only be inferred that this forms an important nutrient resource for *L. terrestris*, there is substantial evidence that earthworms feed selectively on materials with a high nitrogen content.

(c) *Food selection. Lumbricus terrestris, L. rubellus, A. longa, A. caliginosa, A. rosea, E. foetida* and *D. octaedra* all show ability to distinguish between different kinds of litter (Lindquist, 1941). Food selection has been studied mainly in *L. terrestris*, which preferentially selects the leaves it draws into its burrows when offered a choice of different kinds (Table XII). In general,

TABLE XII

Order of preference of *L. terrestris* for leaves of different plant species (from Bornebusch, 1953)

(i)	*Mercurialis perennis, Urtica dioica, Oxalis acetosella, Agrostis* sp., *Sambucus nigra*
(ii)	*Crataegus* sp., *Alnus glutinosa, Ulmus* sp., *Fraxinus excelsior, Prunus padus, Coryllus avellana, Betula* sp., *Acer pseudoplatanus, Carpinus betulus, Ribes* sp.
(iii)	*Prunus serotina, Fagus sylvatica, Quercus robur* s.l., *Q. borealis*
(iv)	*Abies alba, Pseudotsuga taxifolia*
(v)	*Pinus mugo, P. sylvestris, P. nigra* var. *austriaca*
(vi)	*Picea abies, Larix decidua, L. leptolepis*

leaves of mull species such as ash or *Mercurialis* are preferred to those of oak or beech or conifer needles. Darwin (1881) ascribed the order of selection to the shape and texture of the leaves, but in choice experiments where the effect of leaf shape is removed by using uniform-sized leaf discs or short lengths of conifer needle the order of selection is little changed. Wittich (1953) observed that protein rich litters are more readily taken than litters containing less protein, and this is supported by other experiments showing a correlation between the palatability of various litters and their nitrogen content (Fig. 14). However, litters with a high nitrogen content generally also have a high sugar content (Fig. 15) and, as earthworms are capable of detecting sweet tasting substances (Mangold, 1953; Laverack, 1960), this may explain their selection of protein-rich litter.

The palatability of litter may be much increased by a short period of

weathering (Table XIII), and this may result from the breakdown of certain distasteful polyphenolic substances (Fig. 16). Brown, Love and Handley (1963) have recently shown that leaves of spruce, larch, beech and oak, which all produce unpalatable litter, contain condensed tannins which are absent

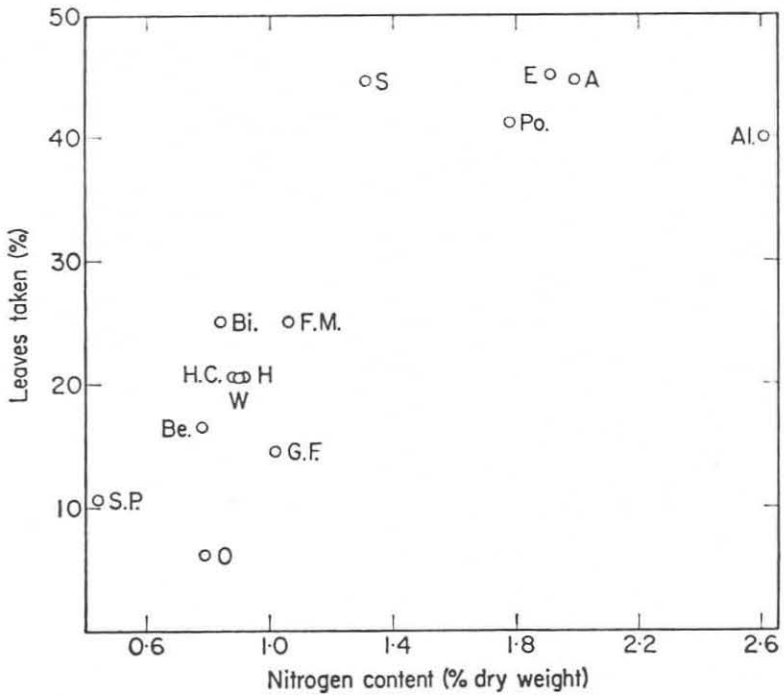

FIG. 14. Palatability of litter in relation to its nitrogen content.
A, Ash; Al, Alder; Be, Beech; Bi, Birch; E, Elder; F, Giant Fir; F.M, Field Maple; H, Hazel; H.C, Horse Chesnut; O, Oak; P, Scots Pine; Po, Poplar; S, Sycamore; W, Walnut.

from *Mercurialis*, nettle, elderberry, ash and Wych elm which are all highly palatable to earthworms. Moreover, it can be shown (Fig. 17) that (+)-catechin, a commonly occurring leaf polyphenol, is repellant to *L. terrestris*, which withdraws from solutions of (+)-catechin at speeds directly related to their concentration.

TABLE XIII

Number of leaf discs removed from the soil surface by *L. terrestris* in laboratory experiments (Satchell, unpublished work)
(6 discs of each kind given nightly for 11 nights)

Duration of weathering after leaf fall	Beech	Oak	Hazel	Birch
—	57	59	77	87
6 weeks	80	74	89	92
12 weeks	88	90	98	101

The increased palatability of oak litter after weathering appears to result from microbial activity. In selection experiments with *L. terrestris* (Table XIV), fresh oak litter discs kept in running tap water for 14 days were not taken in significantly greater numbers than untreated discs, but their palatability was increased considerably by incubation in water at room temperature

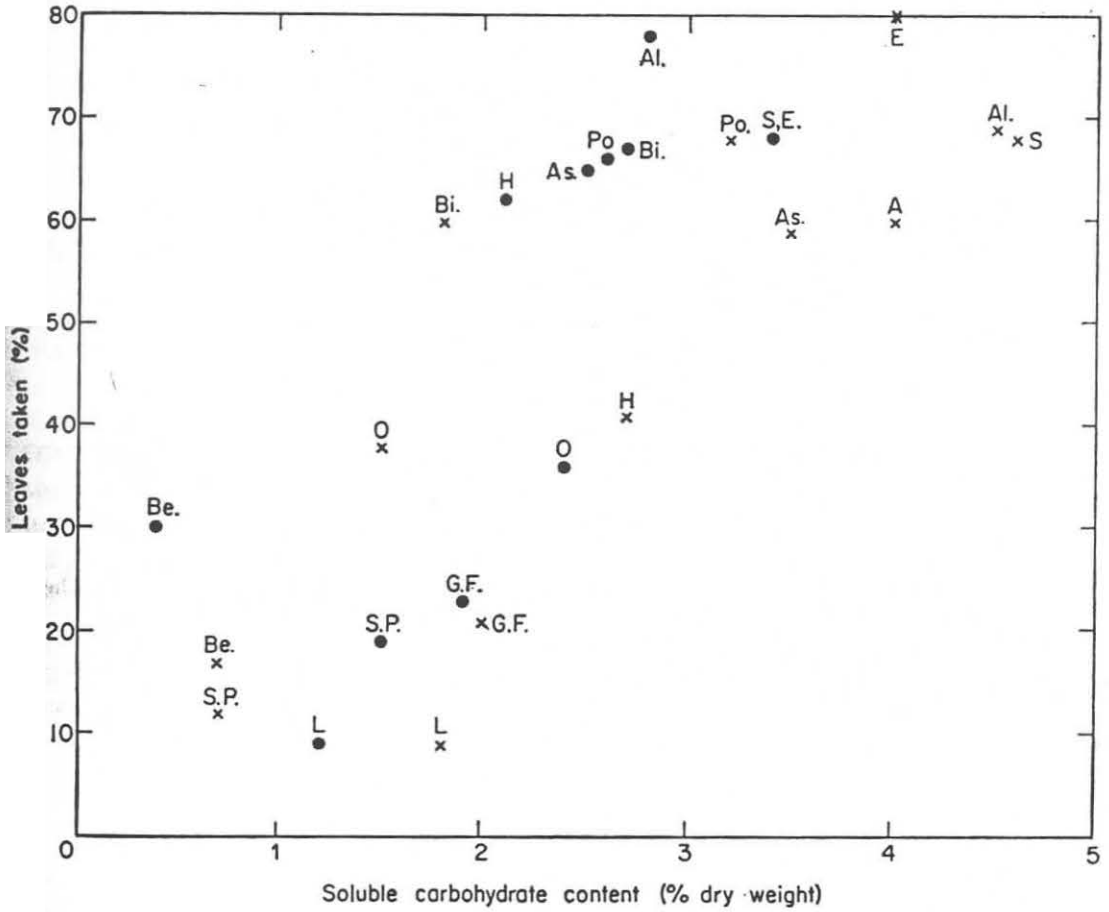

FIG. 15. Palatability of litter in relation to its soluble carbohydrate content. Percentage of leaf discs and conifer needles removed from the soil surface by *L. terrestris* in laboratory experiments.

Six discs or needle lengths of each kind given nightly for 33 nights.

x, Fresh litter. •Weathered litter; As, Aspen; L. Larch. For other abbreviations see Fig. 14.

for 2 weeks following exposure outdoors for 48 hours. It is known that the so-called white rot fungi produce enzymes capable of oxidizing phenols and that *Penicillium solitum* and *Aspergillus niger* can decompose substances such as (+)-catechin (Bocks, Brown and Handley, 1963) and it may be that related microbial enzyme systems degrade the leaf constituents unpalatable to earthworms.

3. *The response of earthworms to soil acidity*

The distribution of earthworms in relation to mull and mor (Tables VI, VII and VIII) appears to be controlled by their response to the pH of their

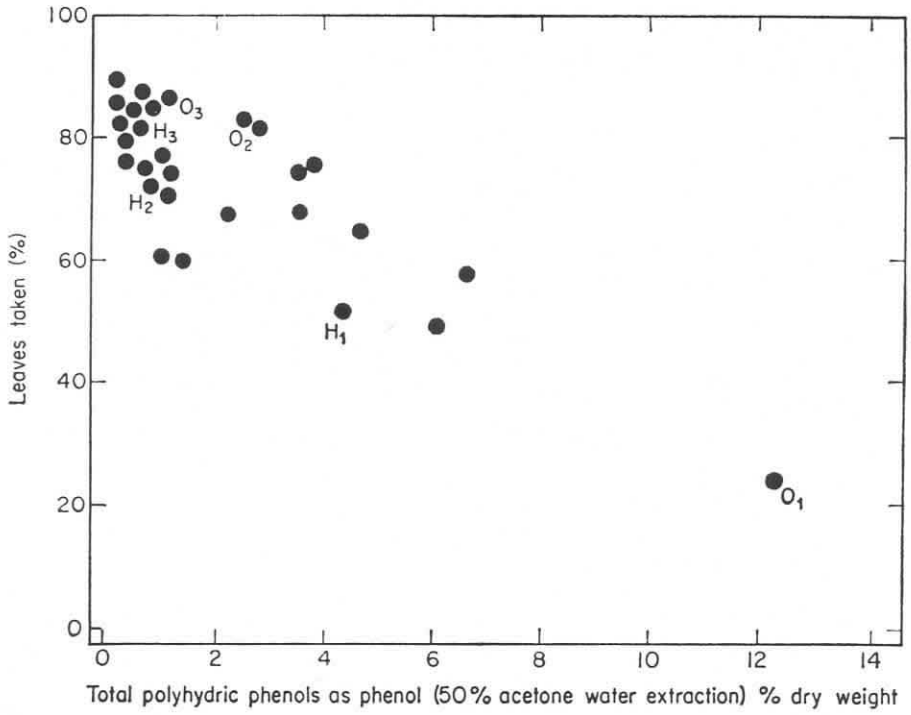

FIG. 16. Palatability of litter in relation to phenolic content. 1, fresh litter; 2, litter weathered for 6 weeks; 3, litter weathered for 12 weeks. For other abbreviations see Fig. 14.

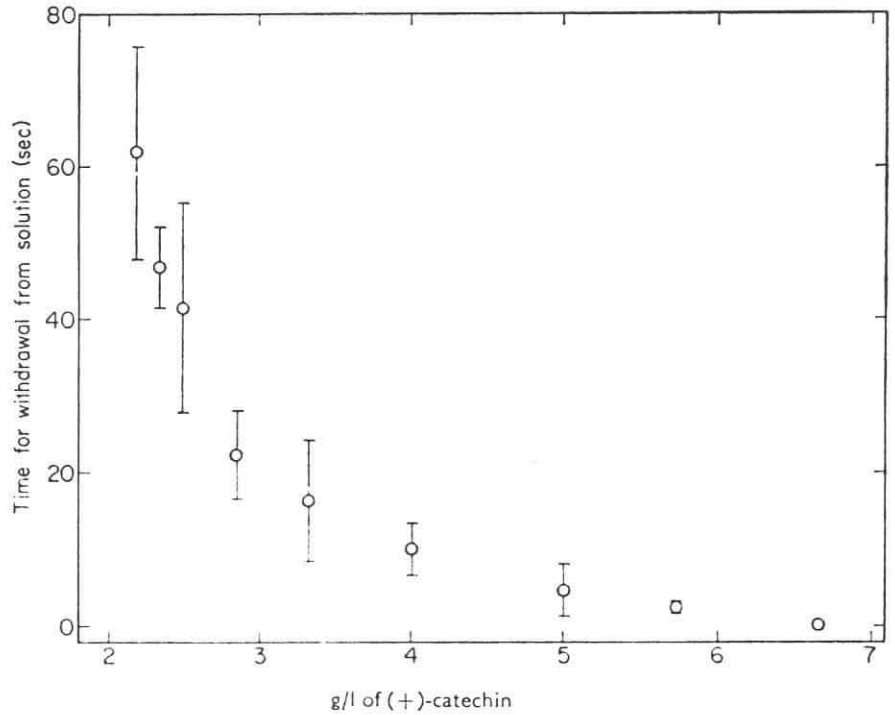

FIG. 17. Reaction of *L. terrestris* to aqueous solutions of (+)-catechin. Means of 5 replicates, and 95% confidence limits.

TABLE XIV

Selection by *L. terrestris* of leached and incubated oak litter discs (Satchell and Lowe, in press)

Disc treatment	Replicate	No. of discs taken out of 50 supplied	
		Treated	Control
14 days in running water	1	15	16
	2	26	16
14 days' incubation in 5 cc water at 17° c after 2 days' exposure outdoors	1	34	12
	2	42	16
14 days' incubation in 5 cc water at 26° c after 2 days' exposure outdoors	1	35	5
	2	42	19

environment. In laboratory experiments the response of different species to solutions of different acidity has been found to correspond with their distribution in relation to pH in nature (Laverack, 1961b). For example, *A. longa* inhabits soils down to pH 4·5, *L. rubellus* soils down to about pH 3·7 to 3·8 and *L. terrestris* soils down to pH 4·1 and occasionally lower. By flooding the body wall of these species with buffer solutions and recording the action potentials in the segmental nerves, Laverack (1961b) showed that the threshold for stimulation in *A. longa* lay between pH 4·6 and 4·4; *L. terrestris* had a threshold at pH 4·3 to 4·1; and *L. rubellus* at pH 3·8 (Fig. 18).

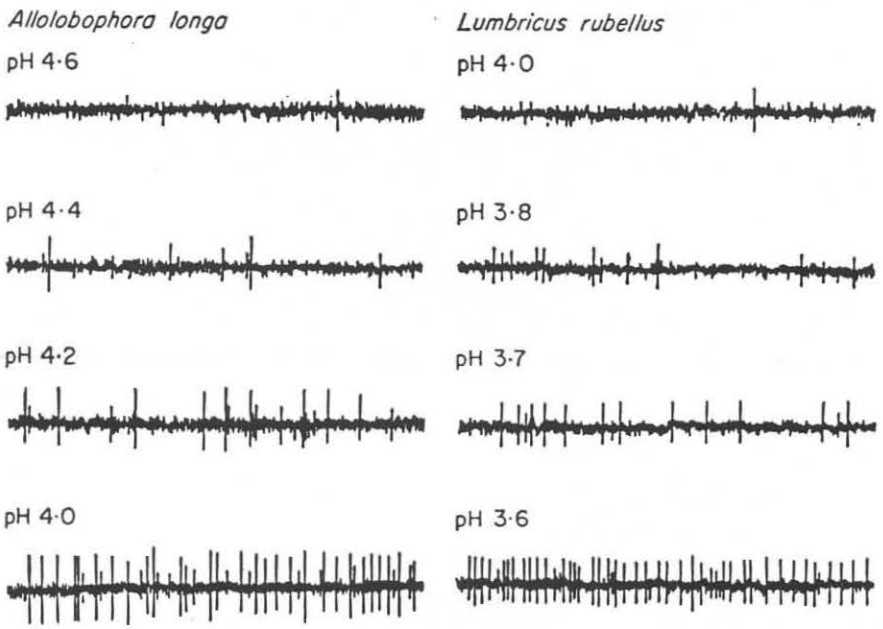

FIG. 18. Oscilloscope recordings of electrical activity in segmental nerves of earthworms stimulated by solutions of different pH (from Satchell, 1960).

Laverack supported this neurophysiological evidence with experiments on behaviour. Specimens of the same 3 species were held so that the anterior segments dipped into buffer solutions. *A. longa* withdrew the prostomium abruptly from solutions of pH 4·4 and below, *L. terrestris* responded similarly at a threshold of about pH 4·0 and *L. rubellus* at about pH 3·8 (Fig. 19). These thresholds correspond to the acidity tolerance of each species in the field. Another type of experiment confirmed this. When *A. longa* and *L. rubellus* were placed in pots of soil of acidities ranging from pH 4·0 to 4·9, *L. rubellus* burrowed into all the soils, but *A. longa* only burrowed into the soils of pH 4·6 and above. On soils of pH 4·4 to 4·0 the *A. longa* searched actively for a time and then became quiescent on the surface, where they eventually died.

It has been customary for many years to ascribe the absence of the larger earthworms from very acid soils to the soils' deficiency in calcium. Calcium

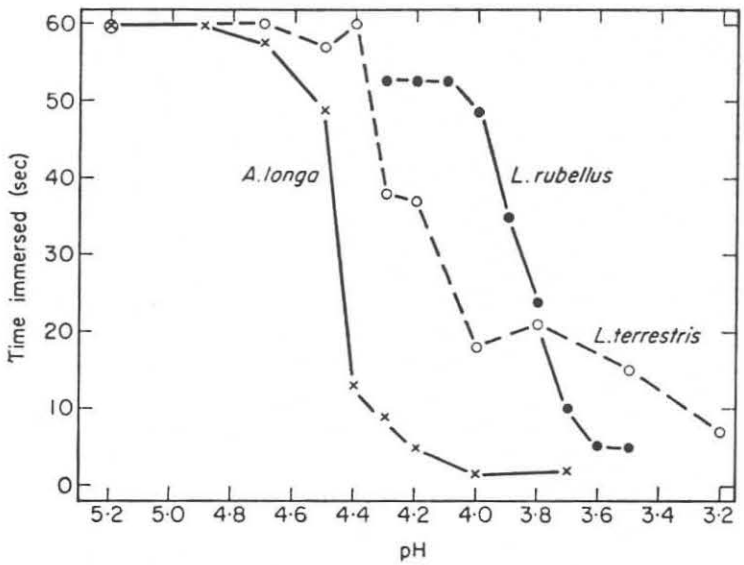

FIG. 19. The average time taken to withdraw the prostomium from acid pH solutions in 3 species of earthworm (from Laverack, 1961b).

is excreted as calcium carbonate from the calciferous glands and plays an important role in earthworm metabolism. The species of earthworms normally found in mull are absent from the calcium-deficient podzols of Rhum although, because of high magnesium content, the soil pH is between about 5·0 and 7·0 (Wragg and Ball, 1964). The availability of calcium or nitrogen or both may limit the earthworm population directly, but the fact that mull species die on the surface of very acid soils without ever ingesting any soil suggests that the immediate cause of their absence from mor soils generally is not a nutritional deficiency but their sensory response to acidity.

4. Distribution in relation to soil moisture

Various behaviour mechanisms by which Lumbricidae avoid desiccation have already been described. Although the inhibition of feeding by drought

(reflected in *Allolobophora* spp. by reduced casting and in *L. terrestris* by reduced surface activity) helps individuals to survive, it reduces population densities by decreasing the rate of cocoon production. The effect of soil moisture on cocoon production by *A. chlorotica* is illustrated (Fig. 20) by

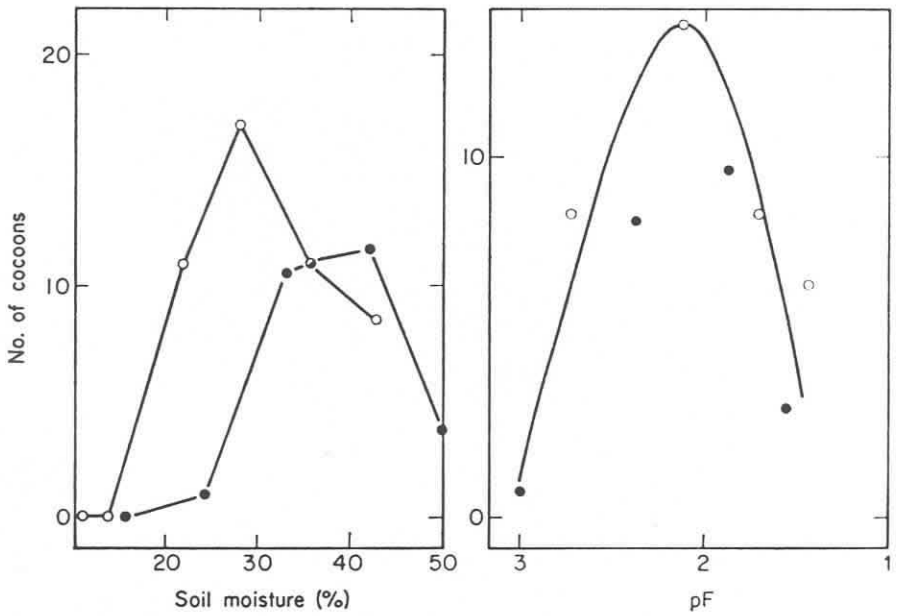

FIG. 20. Relationship between soil moisture and cocoon production by *A. chlorotica* in 2 Rothamsted fields (from Evans and Guild, 1948).
●—● Westfield; o—o, Bones Close

the work of Evans and Guild, who found an optimal soil moisture tension for cocoon production somewhat above the sticky point in the region of pF 2.

The distribution of earthworms in relation to soil types recorded by Guild (1948) (Fig. 21) probably reflects a combination of the effects of soil moisture and available food, but the differences between species in their tolerance of drought are greater than Fig. 21 may suggest. Table XV illustrates the

TABLE XV

Earthworm populations of irrigated and unirrigated plots on Lower Greensand (Woburn, Beds., May, 1960) (adapted from Gerard, 1960)

Species	No./8·9 m² (Sampled by formaldehyde method) Irrigated	Un-irrigated
L. terrestris	231	224
A. longa	3	1
A. chlorotica		2
A. caliginosa	33	0
A. rosea	33	0

striking effect of deficient soil moisture on the earthworm populations of irrigated and un-irrigated plots on sandy soils on the lower Greensand at Woburn (Gerard, 1960). The topsoil species *A. chlorotica*, *A. caliginosa* and *A. rosea* were common on irrigated plots and virtually absent from un-irrigated plots, but *L. terrestris*, which has burrows extending deep into permanently moist soil, was apparently unaffected by the irrigation.

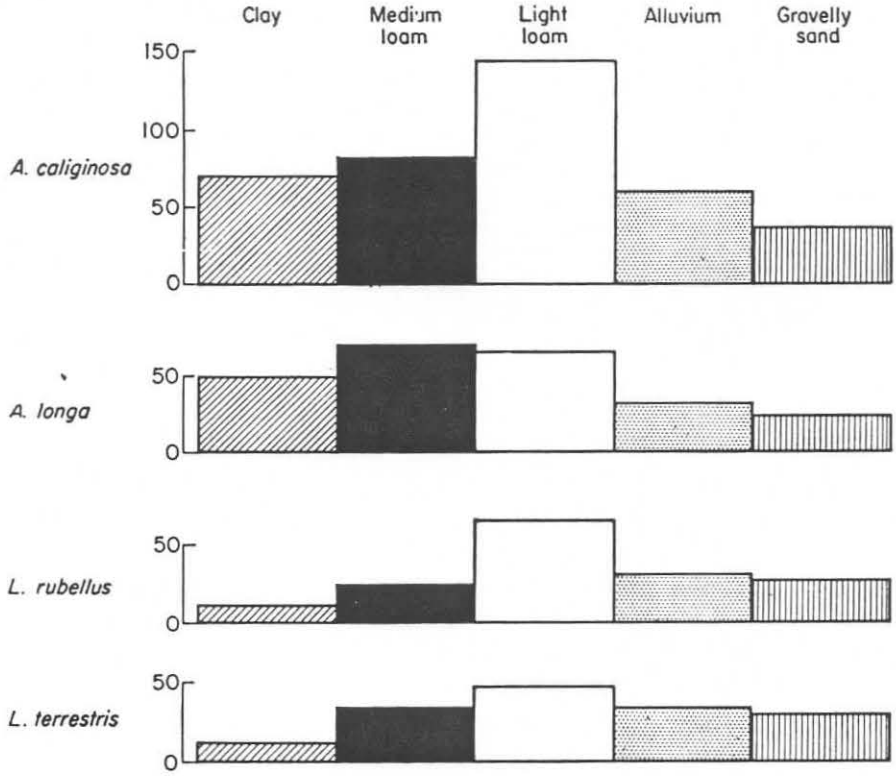

FIG. 21. Density of earthworm populations (thousands/acre) in various soil types in Scotland (adapted from Guild, 1948). ▨, clay; ■, medium loam; □, light loam; ▩, alluvium; ▥, gravelly sand.

The two colour forms of the polymorphic *A. chlorotica* provide an interesting example of the effect of soil moisture on distribution at sub-specific level. *A. chlorotica* inhabits a wide range of habitats from the permanently submerged root zone of *Phragmites* beds in Lake Windermere to forest, field and garden soils. The two morphs are occasionally found together but generally they form separate populations, the green form in wet sites and the pink form in drier sites. Table XVI shows this for soils in northern England. The physiological basis for the different distributions of the two forms has not yet been elucidated (Roots, 1955, 1956).

5. Distribution in relation to soil temperature

In arable soils in continental climates the earthworm population may be largely destroyed by autumn frosts (Hopp, 1947), but it is exceptional under

TABLE XVI

Occurrence of the two colour forms of *A. chlorotica* in relation to soil moisture in summer

	Woodland			Gardens			Upland limestone grassland			Lowland pastures		Marshy ground and beside tarns, streams and rivers					
	Brigsteer (W)	Eggerslack (L)	Witherslack (L)	Kendal (W)	Levens (W)	Merlewood (L)	Kendal Fell (W)	Helsington Fell (W)	Blawith Fell (L)	Sampool (W)	Foulshaw (W)	Kendal Fell Tarn (W)	River Gilpin (W)	Sunbiggin Tarn (W)	Meathop Marsh (L)	Colt Park Spring (Y)	Long Sleddale (W)*
% Green form (Sample size: 100–300 worms)	0	0	0	0	0	0	0	0	8	4	45	91	93	99	99	100	100
% Soil moisture, September 1959	24	22	20	13	21	20	21	17	17	30	26	53	17	52	41	41	41

* (L) = Lancs., (W) = Westmorland, (Y) = Yorks.

grass or forest cover for the soil to freeze deep enough to affect the population. Under natural conditions, the upper lethal temperature determined experimentally as 28° C for *L. terrestris* (Wolf, 1938a; Hogben and Kirk, 1944), 25° C for *E. foetida* and 26° C for *A. caliginosa* (Grant, 1955b), depends on soil moisture (Table XVII). Like terrestrial gastropods, the earthworm can maintain a lower body temperature than that of its surroundings by evaporating body water. At relative humidities above 37% the body temperature of *L. terrestris* does not exceed that of a wet bulb thermometer by more than 2° C (Hogben and Kirk, 1944).

Body temperature may also be controlled to some extent by thermotaxis. In temperature choice experiments with worms conditioned at 20° C, Grant (1955b) found that *E. foetida* moved into temperatures between 15·7° C and 23·2° C and *A. caliginosa* congregated between 10° C and 23·2° C.

In the field, response to temperature changes is probably the main cause of seasonal movement up and down the soil profile (Fig. 22), and in nature it is unlikely that earthworms are ever unable to avoid lethal temperatures or temperatures too high for optimum cocoon production (Fig. 23). Neverthe-

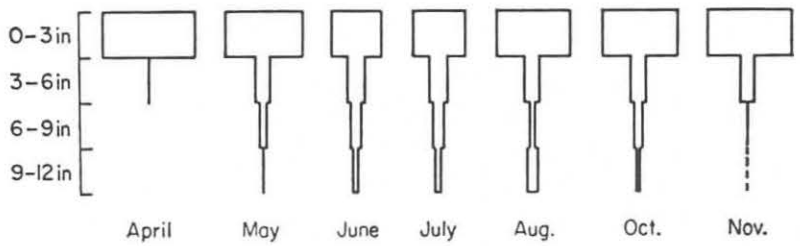

FIG. 22. Seasonal distribution of *Allolobophora* spp. in a pasture field, Rothamsted, 1959 (adapted from Gerard, 1960).

less, soil temperature is of fundamental importance in earthworm ecology because of its effects on motor activity and metabolic rate.

6. *Distribution in relation to soil aeration*

The ability to tolerate submergence differs greatly between lumbricid species. Populations of *A. chlorotica* occur entirely below water in Lake Windermere. Aquatic populations of *A. caliginosa* and *A. longa* are unknown but when offered a choice of water-saturated and air-filled soil a few are always found in the saturated soil. *L. rubellus* occurs in sewage beds but avoids immersion in water when offered a choice (Roots, 1956), while *L. terrestris* and *D. rubida subrubicunda* are never found in aquatic habitats. Whereas all these species can survive many months in aerated water, *Helodrilus oculatus* can live permanently in habitats of very low oxygen tension, such as the mud under the River Thames (Dobson and Satchell, 1956).

The effect of soil aeration on earthworm distribution is at present not well documented although it is undoubtedly important, particularly in moorland,

TABLE XVII
Number of *A. chlorotica* dead and aestivating after 30 days in experimental cultures (initially 10 worms per culture) (from Gerard, 1960)

Soil temperature (°C)	Soil Moisture: Very wet		Moist		Dry		Very dry	
	No. aestivating	No. dead	No. aestivating	No. dead	No. aestivating	No. dead	No. aestivating	No. dead
5	0	0	0	0	1	7	—	10
10	0	0	1	0	3	4	—	10
14	1	0	1	0	2	7	—	10
20	1	0	7	1	4	6	—	10
25	5	1	5	5	—	10	—	10

bog and similar highly organic sites. The distribution of *B. eiseni* and *D. octaedra* appears to be limited in some sites by the minimum oxygen tensions occurring at certain seasons, but this is difficult to demonstrate because factors such as soil water content, the presence of raw humus, the plant cover and soil microflora, which may have independent effects on earthworms, are linked as causes or effects to variations in the soil atmosphere. For example, on Silpho moor, an acid heather moor (see p. 278), dung bait trapping showed (Satchell, unpublished work) that *Bimastos eiseni* was relatively abundant in drier areas but scarce or absent in wetter areas characterized by the presence

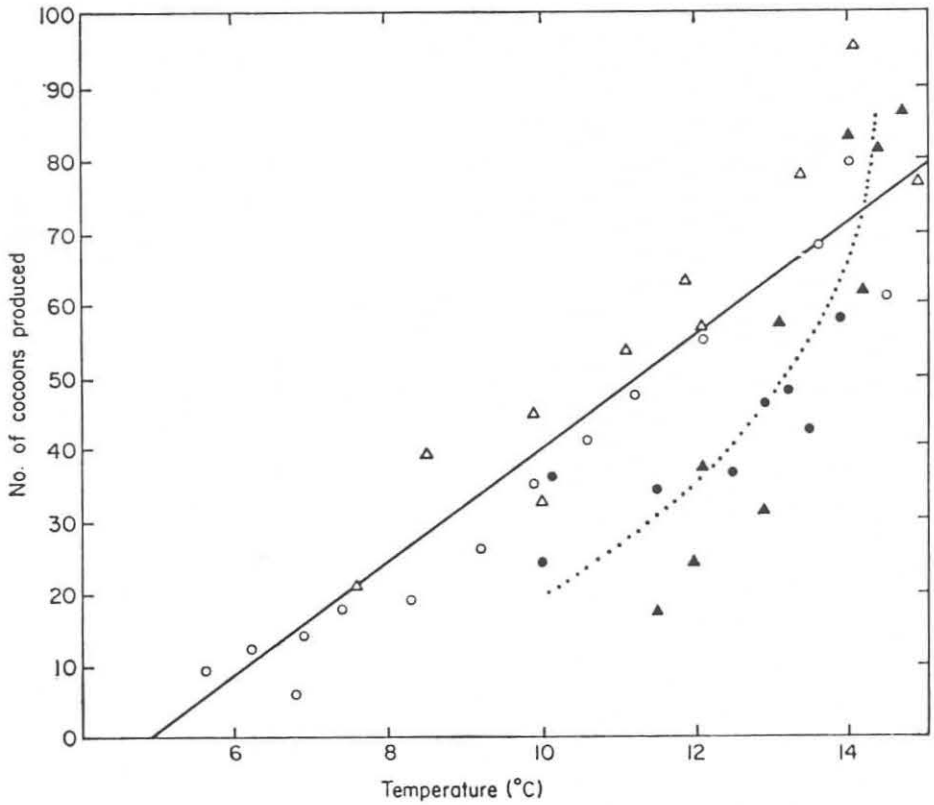

FIG. 23. Relationship between cocoon production by *L. rubellus* and increasing and decreasing temperature (Evans and Guild, 1948).
Increasing temperature, △ (1945), ○ (1946); decreasing temperature, ▲ (1945), ● (1946).

of *Eriophorum*. The calcium and nitrogen concentrations in the upper layers were correlated with the earthworm distribution but could not account for the marked difference between wet and dry areas. However, oxidation-reduction potentials measured after heavy rainfall in November (Fig. 24) showed that extremely low oxygen tensions sometimes occurred in the surface horizons of the wetter areas. As *B. eiseni* can survive in aerated water, it seems likely that low oxygen tensions rather than water were responsible for the scarcity of worms in these areas.

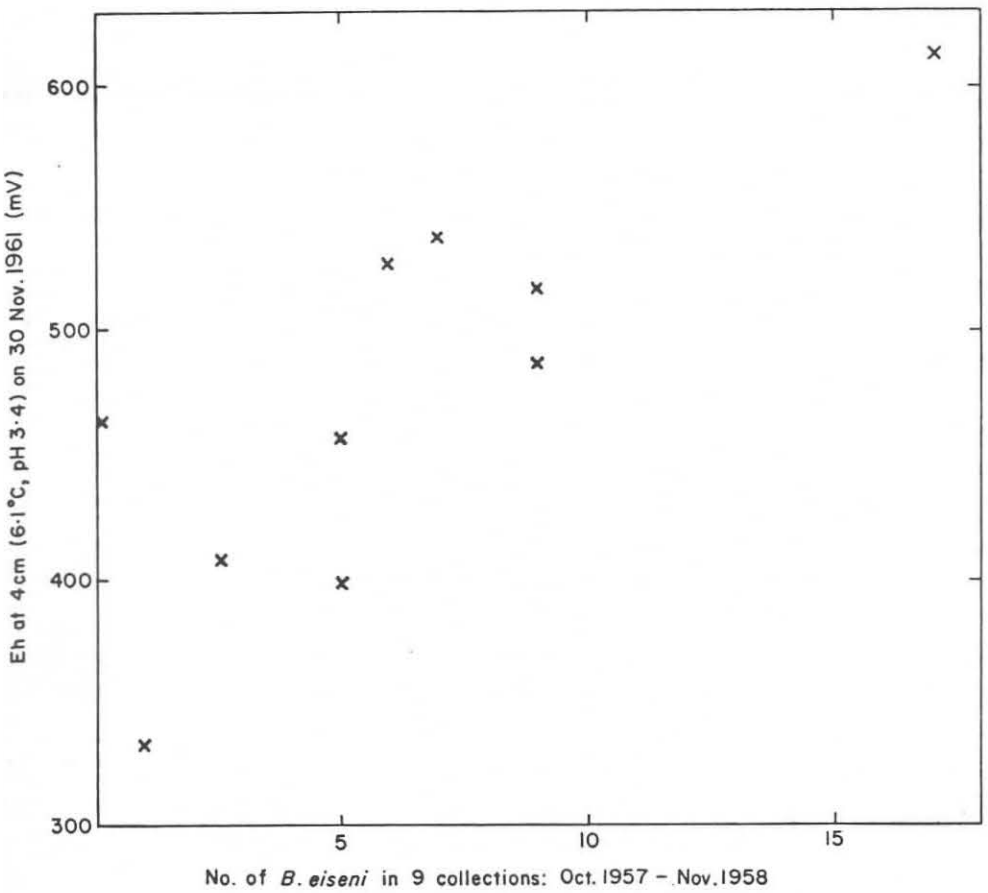

FIG. 24. Distribution of *Bimastos eiseni* in relation to oxidation-reduction potentials at 10 trapping points on Silpho moor, Yorkshire.

IV. EFFECTS OF EARTHWORMS ON SOIL STRUCTURE

A. THE STRUCTURAL STABILITY OF EARTHWORM CASTS

The aeration and water-holding capacity of soil are largely determined by its physical structure: with a good crumb structure water is retained in the capillary spaces within the aggregates, allowing continuous gaseous diffusion between them. Mull is characterized by an aggregated structure, and in defining mull, Kubiena (1953) states, "Practically all the aggregates are earthworm casts or residues of them." Consequently, one of the most important effects of earthworm activity appears to be its influence on the crumb structure of mull soil.

From the evidence of wet-sieving and water-drop stability tests it has been generally agreed by numerous workers (Bassalik, 1913; Joachim and Panditesekera, 1948; Bakhtin and Polsky, 1950; Nijhawan and Kanwar, 1952) that worm casts contain more water-stable aggregates than non-cast soil and, in laboratory experiments, that worm-worked soils are more water stable than unworked soils (Gurianova, 1940; Hopp, 1946; Guild, 1955). The stability

of casts depends on the availability of nutritive plant remains (Hoeksema, Jongerius and Meer, 1956) so that the stability of casts from land under grass (Dutt, 1948; Swaby, 1950; Finck, 1952; Ponomareva, 1953) or lucerne (Gurianova, 1940; Teotia, Duley and McCalla, 1950; Mamytov, 1953) is much greater than that of casts from land under straw crops.

A variety of explanations has been advanced of the way in which water stable aggregates in wormcasts are formed. Ponomareva (1953) suggested that aggregates are simply reinforced mechanically by filaments of vascular bundles from ingested plant remains, whereas Meyer (1943) considered that soil particles in the worm's intestine are cemented together by calcium humate formed from ingested decomposing organic matter and calcite excreted by the calciferous glands. Most workers agree, however, that the stabilizing materials originate from the microbial populations which develop in the faeces in the gut or subsequently in the casts (see p. 313). Because grassland casts contained more water stable aggregates and more bacteria than casts from arable land, Swaby (1950) suggested that bacterial gums glued the soil particles together. He found that pasture soil incubated with a suspension of fresh casts became stabilized with fungal hyphae, but he discounted the importance of this because fungi do not increase in the intestine. Subsequently Parle (1963a), using the sodium saturation technique of Emerson (1954), has shown that the stability of casts of *A. longa*, which is low at first as casts are produced in a semi-fluid state, increases to a maximum after 15 days and thereafter breaks down. The changes in stability with age correspond closely with the development of fungal hyphae (Fig. 25) but do not

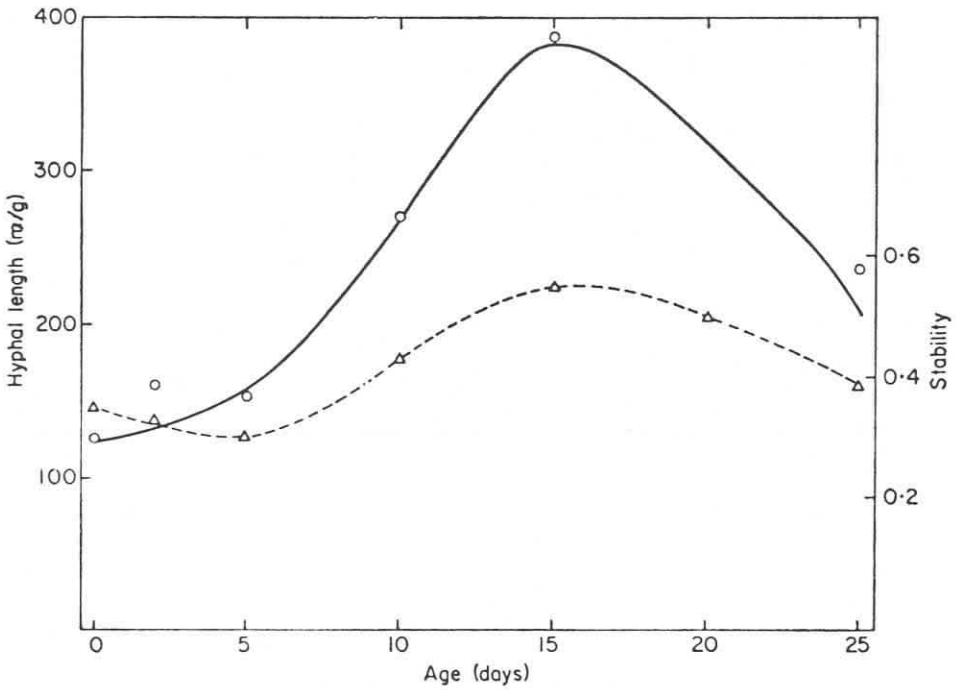

FIG. 25. Length of hyphae in m/g and aggregate stability in ageing casts (from Parle, 1963a). –o——o–, hyphae; --Δ---Δ--, stability.

correspond with changes in the polysaccharide content of the casts. This could mean that the development of fungal hyphae after defaecation is the principal factor in the stability of wormcasts.

In order to assess the importance of wormcasting in the stability of the crumb structure of the soil it is necessary to know both how long the stability of earthworm faeces persists and the rate of faeces production. Evans (1948) calculated the latter on the basis of cast production on the soil surface by *A. nocturna* and *A. longa*. This varied considerably from 1 to 25 tons/acre per annum (approx. 2·5 to 63 m. tons/ha) dry weight. Assuming that, weight for weight, the other species consumed an equal amount of soil but voided it underground, the total soil consumption by earthworms in 8 fields at Rothamsted was estimated at 4 to 36 tons/acre per annum (approx. 10 to 90 m. tons/ha). In four fields this amounted to an annual consumption of 8·7, 5·0, 4·7 and 1·25% of the total weight of the topsoil to a depth of 10 cm which, Evans therefore concluded, would pass through the alimentary tracts of the earthworm population in 11½–80 years. Barley (1959) estimated that an Australian population of *A. caliginosa*, active for 150 days/year, and with a biomass of 80 g/m², would take 60 years to eat a weight of soil equal to that in the top 15 cm of the profile. It is unlikely, however, as these calculations may be taken to assume, that an earthworm population would consume the whole of the topsoil before reingesting any part of it. The rates of ingestion for the four Rothamsted fields, re-calculated on the assumption that the soil was all equally likely to be ingested at any time, are represented in Fig. 26.

If cast stability lasts for less than a month and if, as Evans' figures suggest, less than 10% of the topsoil passes through earthworms annually, then the effect of earthworm activity on the structural stability of soil is likely to be small. However, a number of relevant factors have not yet been sufficiently investigated to warrant this conclusion. For example, the persistence of the stability of earthworm faeces deposited below ground has not been studied, nor has the effect on soil aggregation of burial of plant remains by earthworms been taken into account. Iimura and Egawa (1956) observed a great increase in water-stable aggregates when various soils were incubated in the presence of plant residues. As in the casts studied by Parle, the greatest increase, during the first 16 days, coincided with a vigorous development of fungal hyphae. With the subsequent disappearance of the hyphae the larger aggregates decreased and the smaller aggregates increased in quantity, and the authors suggested that the binding effect of the hyphae was taken over by the cementing effect of bacterial gums. The continual enrichment of burrow walls with mucus and urine could have more influence on aggregating microorganisms than earthworm faeces, but no estimate of the effect of this on soil structure has been made.

In assessing the role of earthworms and soil structure the following comment by Jacks (1963) should be remembered: "It may be justifiable to make the rather sweeping generalization that in the two great plant-ecologically distinguished worlds of the soil, the movement of plant roots is the major structure-forming factor in grassland soils, and the movement of animals in

forest soils. It may be noted that, although the role of earthworms in helping to create the crumb structure of Russian chernozems has been accepted since the time of Dokuchaev, these animals do not commonly occur in North American prairie soils. Crumb-mull structure can be produced in grassland soils without earthworms though they appear to be essential for its formation in at least temperate forest soils."

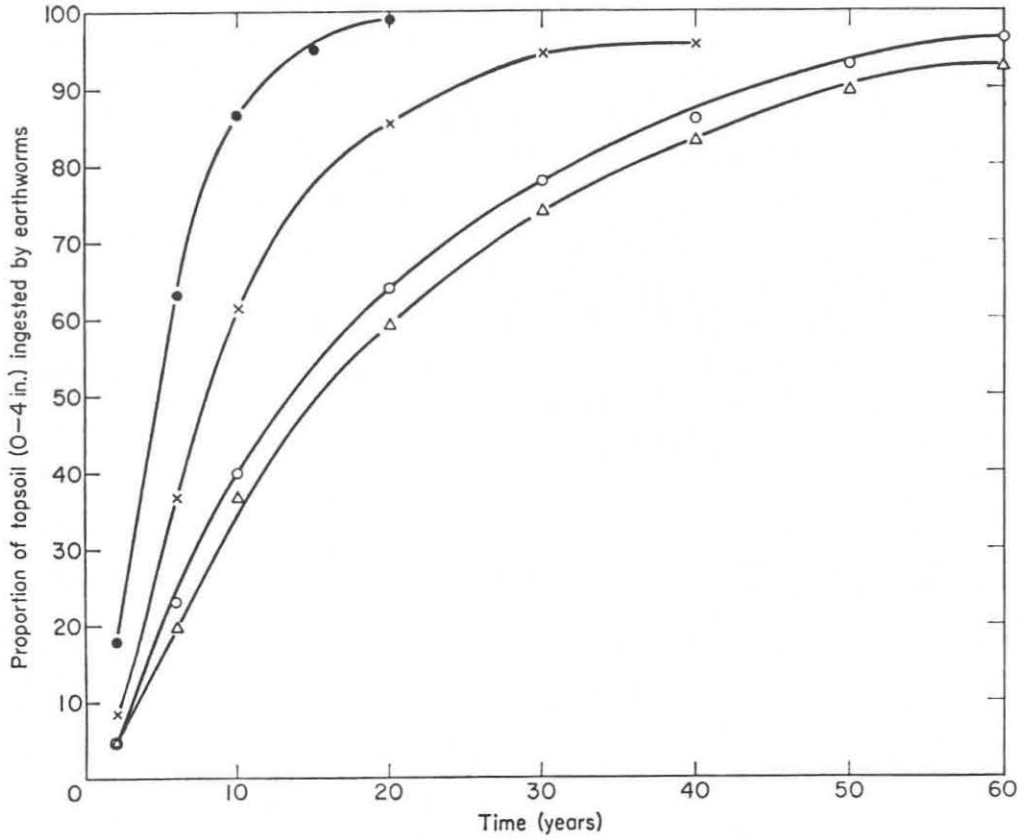

FIG. 26. Rate of turnover of topsoil in 3 grass fields at Rothamsted (recalculated from Evans, 1948).

•, Hypothetical population of 200 g/m²; ×, Parklands; o, Pastures; △, Great Field III.

B. The Effect of Burrows on Soil Aeration and Drainage

The space occupied by earthworm burrows may account for about two-thirds of the air capacity of some soils, and Stöckli (1949) claimed that the volume of earthworm tunnels under grass was as much as 0·05 cc/cc of soil. However, species which defaecate below ground can only open the soil at one point at the expense of consolidating it at another or filling in existing air spaces and, apart from effects on crumb structure, the only activity which can increase soil air space under field conditions is surface casting. Evans' data for cast production at Rothamsted suggest that the volume of soil ejected annually onto the surface by earthworms amounts to only about 0·5 to 6·0%

of the soil in the top 10 cm, the total pore space amounting to 40 to 59% of its volume. Since the rate of casting on the Rothamsted pastures appears to be about average for western Europe, it seems that the effect of earthworms on soil aeration is of only minor importance.

The effect of worm burrows on drainage may, however, be considerable. Slater and Hopp (1947) have shown that infiltration is generally much faster in field soils with high earthworm populations than where populations are low. Although it is difficult to believe that earthworm populations were the only differing factor in their sites, their results are supported by Guild's (1955) laboratory experiments, in which he found that water passed through containers of light sandy soil in 2 days when the soil was worm-worked and in 8 days in the absence of worms. In a number of laboratory experiments (Kahsnitz, 1922; Archangels'kii, 1929; Hopp and Slater, 1948), where yields from plants grown in containers have been higher in the presence of earthworms, the increase has been attributed to improved aeration and drainage. In an apple orchard in Cambridgeshire, Raw (1959) counted an average of 18·5 *L. terrestris* burrows opening at the surface per quadrat of 4 ft². If the average diameter of such burrows is reckoned as $\frac{1}{4}$ in, this would be equivalent in cross section to a drainage pipe 1·75 in (44 mm) in diameter in each metre square.

V. CONSUMPTION OF PLANT LITTER BY EARTHWORMS

A. Comparison of Consumption by Laboratory and Field Populations

The quantity of plant litter and other organic materials eaten or buried by earthworms is difficult to estimate, but several lines of evidence (see, for example, p. 278) suggest that where earthworms flourish the amount of organic matter they consume is limited by the availability of supplies rather than their capacity to ingest it. Laboratory data for a number of species illustrate this: Guild (1955) fed cultures of *A. longa*, *A. caliginosa* and *L. rubellus* for 2 years on cow dung and calculated the average dry weight of dung consumed per worm per annum. The weights obtained for the 3 species were respectively 35 to 40, 20 to 24 and 16 to 20 g. Consumption of dung by immature specimens of *A. caliginosa* at the rate of 80 mg oven dry matter/g fresh body weight, almost twice that found by Guild for this species, has been recorded by Barley (1959). Guild calculated that the annual consumption of dung by a moderate density field population of 100,000 adults acre (approx. 25/m²) each of *A. longa*, *A. caliginosa* and *L. rubellus* would be about 7 to 8 tons/acre (approx. 17 to 20 m. tons/ha) with a total consumption, allowing for immature individuals, of about 10 to 12 tons/acre (approx. 25 to 30 m. tons/ha). Cows produce about 52 lb (approx. 24 kg) dry weight of dung daily and if, say, two-thirds of this fell on the fields of a dairy farm stocked at a density of 1 cow/2 acres (0·8 ha), the amount falling annually to the pasture would be of the order of $2\frac{1}{2}$ to 3 tons/acre (approx. 6 to $7\frac{1}{2}$ m. tons/ha) or about one-quarter of the estimated potential consumption by the earthworm population.

A similar excess of laboratory consumption over field supplies is suggested by the quantity of leaf litter eaten by earthworms under experimental conditions. Franz and Leitenberger (1948) fed *L. rubellus* on hazel litter and recorded an average daily consumption of 20·39 mg dry weight per worm, about 27 mg/g fresh weight of worm. Van Rhee (1963) fed alder leaves and orchard and grassland vegetation to 6 species of earthworms and from 16 trials found an average food consumption of 27 mg/g fresh weight of worm. Needham (1957) fed *L. terrestris* on elm leaves and found a maximum consumption of 80 mg/g worm per day and an average of about one-third of this, similarly about 27 mg/g per day. In the first experiment the hazel litter was collected fresh, air dried and fed in this relatively unpalatable state, and in Needham's experiment a number of worms lost weight. The rate of litter consumption under optimal conditions would therefore seem likely to be higher than 27 mg/g per day.

The weight of leaves falling annually in temperate deciduous woodland is generally of the order of 3,000 kg/ha (Galoux, 1953). A population of *L. terrestris* such as that of Merlewood Lodge Wood, if it fed at the rate of 27 mg/g per day, would consume the entire annual leaf fall in about 3 months. Leaves may in fact, under favourable conditions, be removed from the ground surface by earthworm action, if not actually ingested, at rates similar to this, as illustrated by Raw's (1962) studies of litter disappearance in apple orchards. In one experiment apple leaves were placed under netting in amounts equivalent to 2,000 kg/ha in a cultivated orchard containing approximately 168 g/m^2 of *L. terrestris*. After 2 months (8 February to 8 April, 1960) only 0·5% by weight of the leaves remained on the surface, all but 14 out of 1,000 leaves having been buried by earthworms. The rate of disappearance, including loss by microbial decomposition while on the surface, calculated from the initial weight of the leaves and the number pulled into earthworm burrows, appears to have been approximately 20 mg/g per day. Data for another orchard under grass with a *L. terrestris* biomass of 53·03* g/m^2 yields the same rate over a period of 1 month (27 February to 31 March, 1961). The rate of leaf removal by *L. terrestris* is affected, however, by soil temperature, the quantity of leaves present, and the availability of alternative food resources; the average rate for a series of five orchards during three winters was approximately 5 mg/g per day (Figs 27, 28). The low average rate of activity reflects the low average soil temperature, which was 5·0° C at 30 cm depth.

No comparable data are available for forests, but the work of Bocock *et al.* (1960) demonstrates the different rates of litter disappearance in woodland sites with differing earthworm populations. Ash and oak litter was put out at leaf-fall in coarse meshed nets on two sites, on a moder with a low density earthworm population in which *Bimastos eiseni* was the only species found, and a mull containing numerous *L. terrestris* and *A. rosea*. On the latter site, ash litter disappeared so rapidly that, after about 6 months, only a few midribs remained. Both ash and oak leaves on the moder lost weight slowly and,

* Estimate based on 15% loss of weight on preservation in formalin.

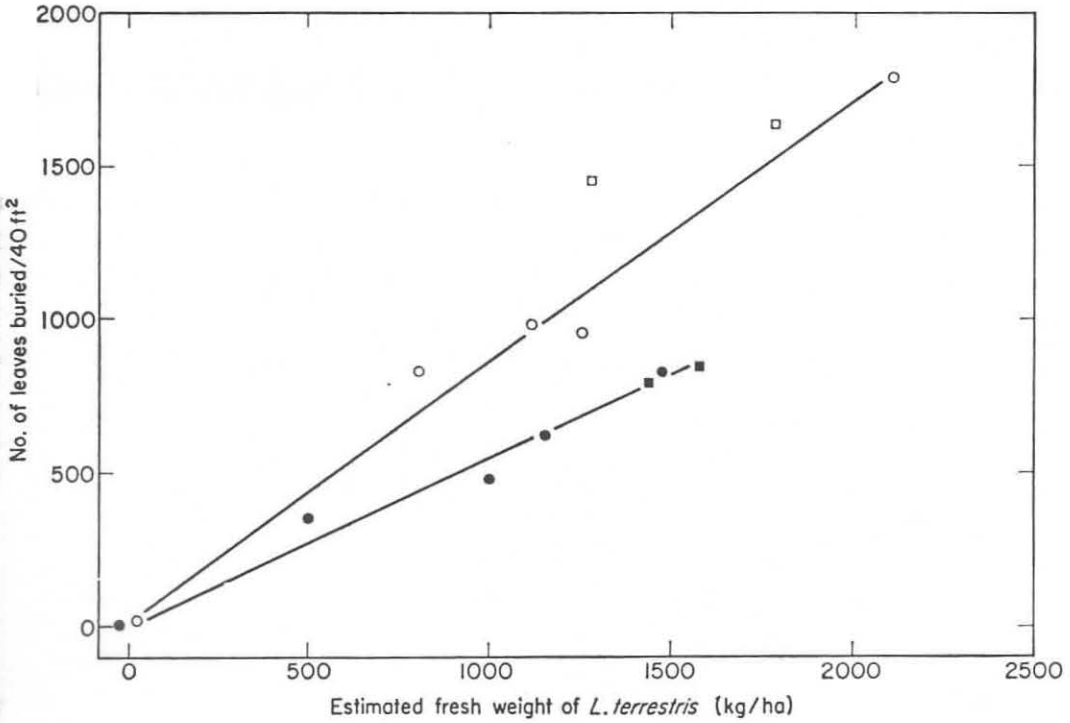

FIG. 27. Effect of initial amount of leaf litter on amount buried by *L. terrestris* in 5 grass and 2 arable orchards. •, cages with 100 leaves; ×, cages with 200 leaves; ■, □, arable orchards, regression lines for grass orchards only (adapted from Raw, 1962).

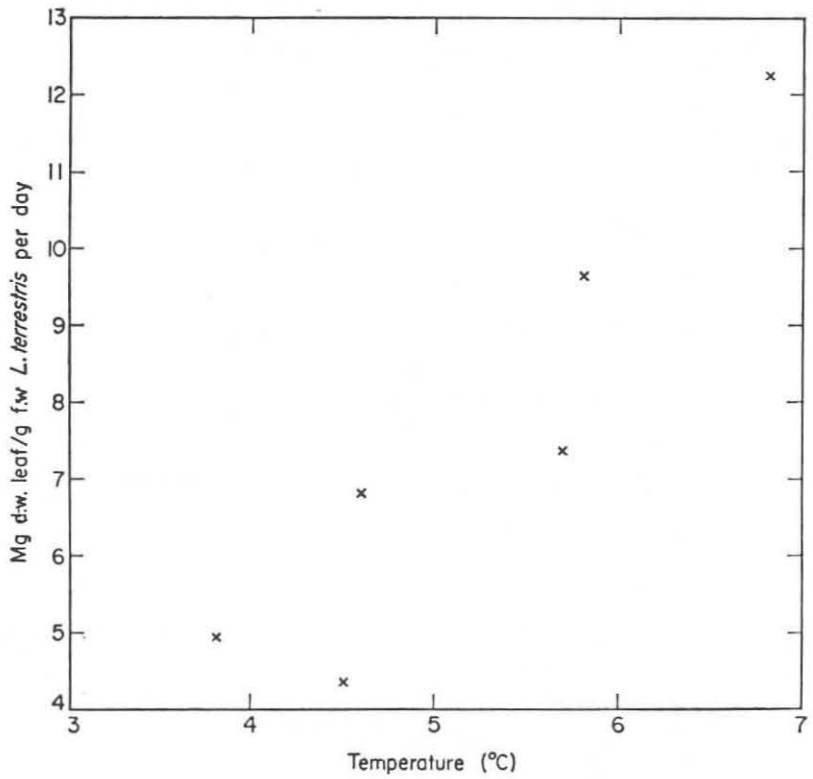

FIG. 28. Weight of leaves buried in apple orchards (and loss of weight prior to removal) during periods of 5–12 weeks (adapted from Raw, 1962).

in contrast to the mull, few leaves were removed from the nets. The oak leaves on the mull also disappeared slowly and it was recorded that, during the 6 to 8 months following leaf fall, leaves of ash, hazel and birch in the natural litter layer (Fig. 29) were drawn into the burrows of *L. terrestris* in preference to oak leaves. Subsequently, both the natural oak litter and the experimental material were attacked by earthworms. The disappearance of discs cut from growing oak and beech leaves and buried 2·5 cm deep in a recently ploughed

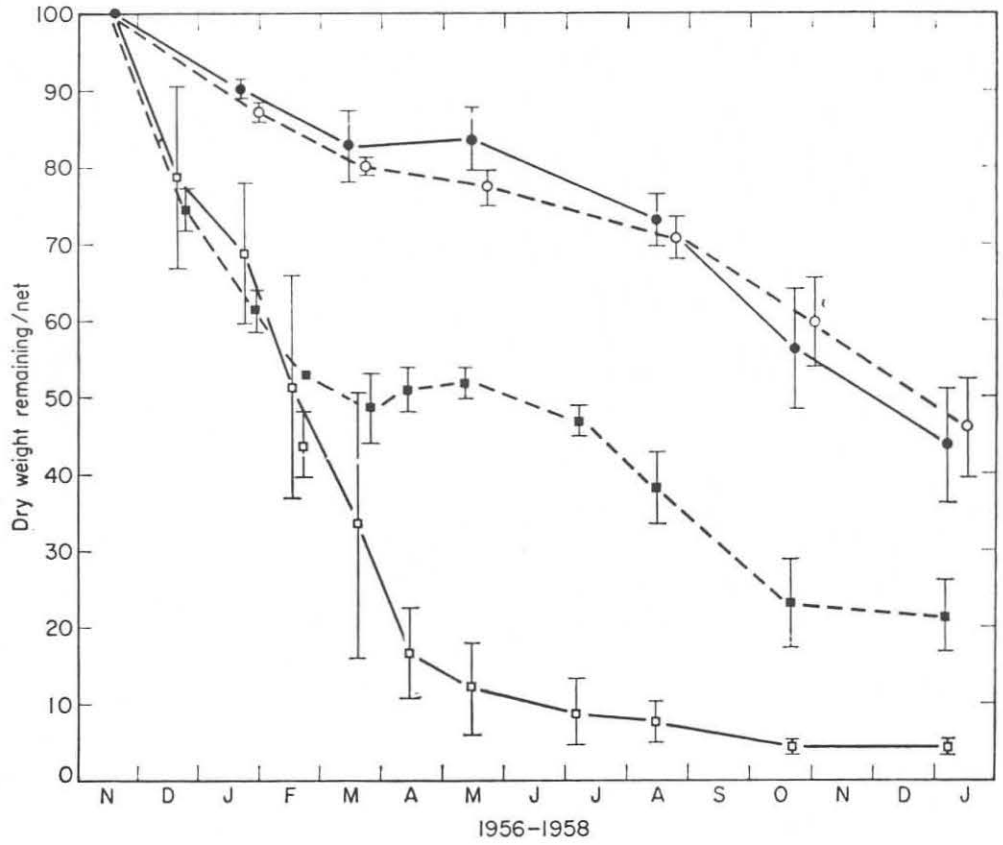

FIG. 29. Disappearance of oak and ask leaves from nets on sites with contrasting humus types. Percentage of the original dry weight remaining per net. Means ±95% confidence limits (from Bocock *et al.*, 1960).
•—•, Oak on mull; o ··· o, Oak on moder; □—□, Ash on mull; ■—■, Ash on moder.

pasture field containing a small earthworm population (39 g/m²) is illustrated in Fig. 30. About 95% of the oak had disappeared after 9 months from nets with a large mesh but only 40%, estimated on a leaf area basis, from nets with a mesh size too small to admit earthworms (Edwards and Heath, 1963).

B. The Effect of Earthworms on Litter Disappearance

The development of surface organic horizons is often attributed to the absence of earthworm activity. In many cases other factors are more important but the classical experimental plots of Park Grass, Rothamsted provide an example where the effects of earthworm activity may be fairly

clearly defined. As a result of repeated applications of ammonium sulphate the acidity on some plots has eliminated the earthworm population completely and a thick mat of dead vegetation has developed. It has been suggested that the mat of partly decomposed herbage which accumulated was formed because the intense acidity of the soil retarded the decay of organic matter. This is evidently only part of the explanation, for when the organic matter is mixed with the soil it decomposes readily. Probably the primary cause of the formation of a "mat" in these plots is the complete absence of worms to pull the dead herbage into the soil (Richardson, 1938). A comparable accumulation of organic matter in an orchard under grass

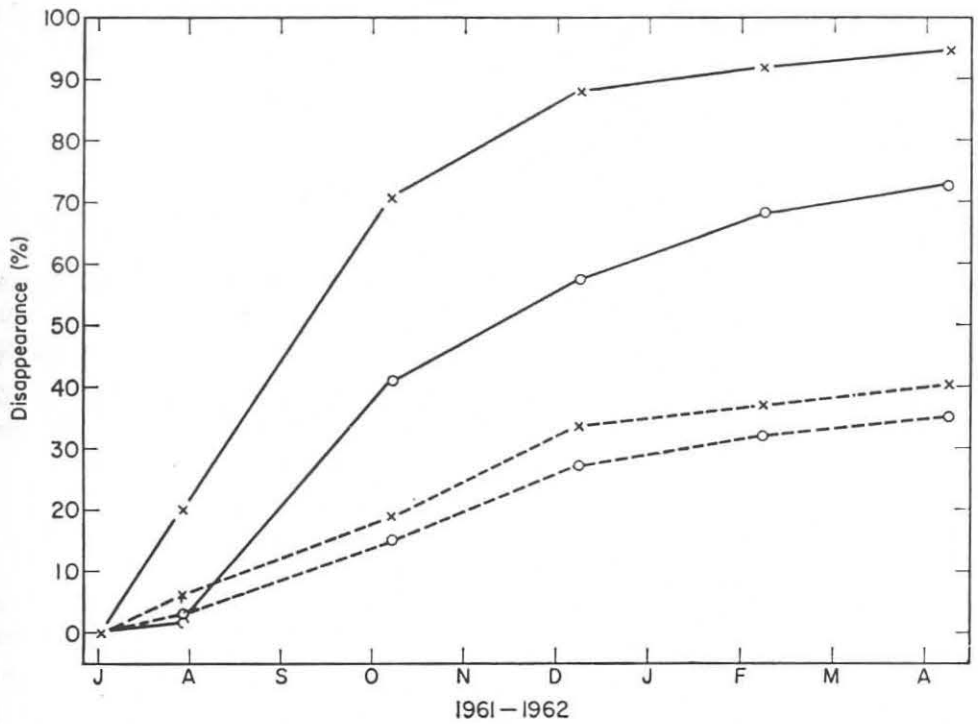

FIG. 30. Decomposition of leaf discs by soil animals (from Edwards and Heath, 1963). ×—×: oak leaf discs in 7 mm mesh bags; o—o: beech leaf discs in 7 mm mesh bags; ×---×: oak leaf discs in 0·5 mm mesh bags; o---o: beech leaf discs in 0·5 mm mesh bags.

occurred where the earthworm population had been poisoned by copper sulphate spray (Raw, 1962). Both soil profiles showed the clear disjunction between the organic layer and the mineral soil and the absence of crumb structure which are characteristic of mor soil. In New South Wales, Australia, irrigated pastures from which earthworms are absent may accumulate surface mats up to 4 cm thick and containing as much as 147 kg/ha of organic nitrogen. In some of these sites where earthworms have been introduced experimentally, the mixing of voided earth with the litter has led to the disappearance of the mat as a discrete layer (Barley and Kleinig, 1964).

The decomposition curves presented in Fig. 29 for leaf litter on a moder site

suggest that where there are few earthworms or other large litter-feeding invertebrates, even such a readily decomposed material as ash litter would tend to accumulate in a North European climate. Whether the resulting humus form would be like that of mor formed from oak, beech or conifer litter is unknown but seems unlikely in view of the difference in the polyphenolic constituents of the materials. Handley (1954) states, "There are indications that some undetermined properties of the vegetable debris control the soil fauna, so that the soil fauna cannot be regarded as a primary determining factor in the formation of mull and mor." Studies on the palatability of litter to earthworms reported on p. 281–3 and the responses of earthworms to environmental acidity (described on p. 283–6) support this view. It appears that the conditions of site and vegetation which tend to produce mor humus tend also to decrease earthworm populations and so to accelerate the accumulation of surface organic horizons.

VI. EFFECTS OF EARTHWORMS ON THE CIRCULATION OF PLANT NUTRIENTS

Wormcasts are usually richer than the surrounding soil in exchangeable calcium, potassium and available phosphorus (Lunt and Jacobson, 1944; Ponomareva, 1950). This provides evidence that earthworms feed selectively but tells us nothing about the effect on soil of passing through an earthworm's intestine. The effect on calcium, potassium and phosphorus availability is, in fact, unknown.

A. Effects on Nitrogen Mineralization

A provisional assessment can be made, however, of the effects of earthworm activity on the availability of nitrogen in the soil. About half the nitrogen excreted by earthworms is in the form of muco-proteins secreted by gland cells within the epidermis. The other half is a fluid urine containing ammonia and urea and possibly uric acid and allantoin, their proportions depending upon the species of worm and whether it is fasting or feeding (Needham, 1957). All these substances are either soluble in soil solution or rapidly become so as a result of microbial action. In an experiment with young *A. caliginosa* kept in a mixture of soil and ground clover leaves, Barley and Jennings (1959) showed that 6·4% of the non-available nitrogen ingested was excreted in forms available to plant roots.

The body tissue of earthworms, of which up to 72% of the dry weight is protein (Lawrence and Millar, 1945), decomposes rapidly at death and provides a further source of readily mineralized nitrogen. Fig. 31 illustrates the course of nitrogen mineralization of dead *L. terrestris* decomposing in jars of garden soil at 12° C under laboratory conditions. The amount of nitrogen added to each jar was calculated from the weight of the dead earthworms and analysis of a sample of them, and the proportion of worm nitrogen subsequently accounted for in mineralized forms was determined by comparing

the soils to which dead worms had been added with controls without worms. After 2 to 3 weeks the worms had disappeared completely and nitrogen fractions in the soil were roughly in equilibrium. Of the nitrogen added as worm tissue about 25% was present as nitrate, about 45% as ammonia and about 3% as soluble organic compounds. Of the approximately 27% unaccounted for, a little was probably held as undecomposed elements of the chaetae and cuticle and the remainder mainly as microbial protein.

Figure 31 also shows some results from a similar experiment (Russell, 1910) in which the decomposition of dead earthworms in jars of soil was recorded. The two experiments suggest that a large part of the nitrogen of

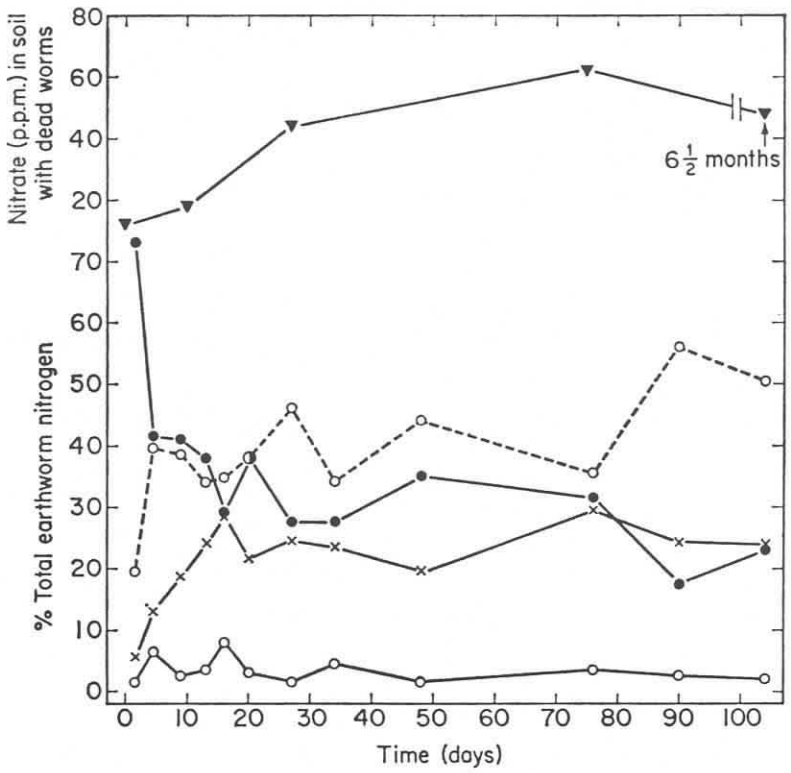

FIG. 31. Mineralization of nitrogen from dead *L. terrestris* (data from Satchell (unpublished) and from Russell, 1910).
o—o, Soluble organic N; ×—×, Insoluble organic N; o ··· o, Extractable NH_4–N; •—•, Residual N.

decomposing earthworms may become adsorbed onto soil colloids as ammonia with nitrification either becoming completely inhibited or proceeding very slowly. This may have arisen in the experiments from the aeration conditions of the soil and Harmsen and van Schreven (1955) point out that in most soils only a minor part of the total amount of NH_4-ions is available for nitrification, varying between none and about 30%. Whatever may be the rate of nitrification of earthworm nitrogen, it seems likely that under normal conditions a minimum of about 70% of the nitrogen in dead earthworm tissue, and probably considerably more, becomes mineralized in 10–20 days.

If it is assumed that earthworm tissue decomposes without significant loss of nitrogen to the atmosphere, an approximate estimate of the amount of

earthworm nitrogen mineralized in a year can be made for a particular population. A first attempt at such an estimate has been made by Skellam and Satchell (Satchell, 1963) for the Merlewood Lodge Wood population of *L. terrestris* (referred to on p. 278). From arguments based on the size structure of the field population and the growth rates of specimens from it reared in culture, the weight of tissue produced in 1 year was estimated to be about 3 times the average weight of the population, about 364 g/m^2. The nitrogen content of *L. terrestris* is about 1·75% of the fresh weight so that, on the steady state assumption that the amount of dead tissue returning to the soil is equivalent to the amount of live tissue produced, the nitrogen returned to the soil as tissue would be of the order of 6 to 7 g/m^2.

A further estimate was made of the amount of nitrogen excreted by this population on the basis of laboratory data obtained by Needham (1957). Needham estimated the rate of excretion by *L. terrestris* fed on elm leaves as 269 μg of nitrogen/g fresh weight of worm per day at 23° C. When adjusted for the observed soil temperatures in Merlewood Lodge Wood (employing provisionally the standard Krogh respiration curve) and applied to the estimated monthly mean biomass values for the population, this yielded an estimated nitrogen output for 1 year of 3·3 g/m^2. The joint yield of nitrogen from excreta and dead tissues from this population would appear therefore to have been about 100 kg/ha in 1 year, about twice the annual uptake of nitrogen by agricultural crops and several times the amount retained annually by tree crops.

What is the effect of this impressive turnover on the ecosystem? Is the availability of the nitrogen in earthworm excreta outweighed by the immobilization of a precious nutrient in the earthworm biomass? The evidence from which such questions could be answered scarcely exists, but if we suppose that leaf litter in mull woodland becomes humified in about 1 year and that a steady state prevails, mineralization of humus proceeding at the same rate as humification, then, as *L. terrestris* survives on average about 1 year, it appears that the supply of available nitrogen will be not much different whether it derives from earthworm tissue or from plant remains decomposed by microbial action. The acceleration of mineralization of plant litter on conversion to earthworm excreta appears, however, to be a bonus on this system. It will be seen, moreover, from Fig. 32 that in three woodland populations sampled in different years the maximum output of excreted nitrogen apparently occurs in early summer at the time of maximum nitrogen demand for plant growth. However, it should be remembered that some assumptions on which these estimates are based, notably that excretion rates are related to soil temperatures in the manner of the Krogh respiration curve, though reasonable, are not yet verified.

There appears to be a vacant niche in temperate forest soils for a holothurian-like earthworm, feeding in the subsoil on low grade organic matter, of large size, occupied mainly by intestine, conserving its energy by a sluggish subsurface existence and its protein supplies by a low reproductive rate and great longevity—in fact, a holarctic equivalent of the 4 ft long Australasian

megascolecid *Spenceriella gigantica* (Lee, 1959). However, the ideal litter feeding animal, from the point of view of obtaining the fastest return of available nitrogen to the ecosystem and narrowing the C:N ratio of plant residues, would combine a high metabolic rate with a short life span. *Eisenia foetida*, the brandling of compost and dung heaps, with a nitrogen excretion rate of 402 μg/day per gram of worm (Needham, Table XVIII) is probably the earthworm most nearly approaching this ideal.

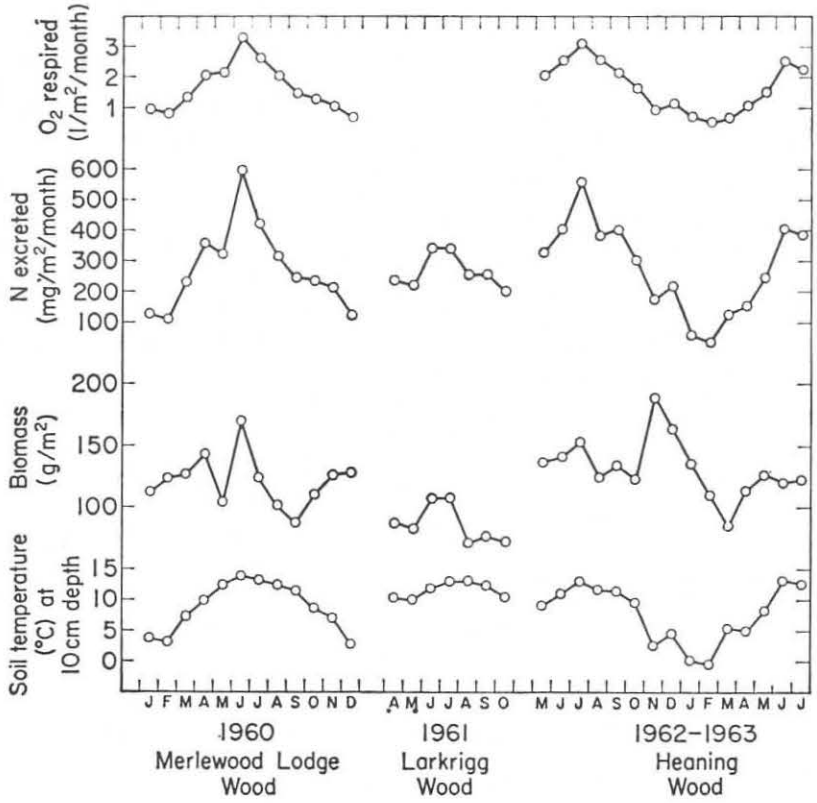

FIG. 32. Estimates of oxygen consumption and nitrogen excretion by 3 woodland populations of *L. terrestris*.

B. EARTHWORM METABOLISM AND ITS EFFECT ON THE C:N RATIO OF SOIL ORGANIC MATTER

The C:N ratio of organic matter added to the soil is of primary importance to the course of mineralization; generally only material with a C:N ratio of 20:1 or lower can directly provide mineral nitrogen (Harmsen and van Schreven, 1955). The following C:N ratios of freshly fallen leaves of common forest trees are given by Wittich (1953): Elm 24·9, Ash 27·6, Lime 38·2, Oak 42·0, Birch 43·5, Rowan 54·0, Scots Pine 90·6. The effect of earthworms in narrowing the C:N ratio of plant remains is not easy to assess directly because, in experimental cultures, earthworms not only metabolize carbon themselves but also increase organic matter decomposition by stimulating

TABLE XVIII

Nitrogen excretion rates of Lumbricidae feeding on elm leaves
Output at 23° C μg/g per day (Needham, 1957)

Species	Ammonia + amino N	Urea	Total N
E. foetida	156·5	48·3	401·8
L. terrestris	54·0	40·8	268·8
A. caliginosa	37·4	19·9	87·5

microbial activity (see p. 317). However, a rough estimate of the minimum carbon consumption of earthworm populations can be calculated from respiration data. Until better estimates are available this may be useful for a provisional comparison with estimates obtained similarly for other faunal groups. The principal factors known to affect earthworm respiration, and hence the validity of such an estimate, are briefly described below:

1. Factors affecting earthworm respiration

(a) *Activity.* It is customary in respirometric studies of animals the size of earthworms to measure the basal or resting metabolism, and the data presented in Fig. 33 may be expected to refer to basal metabolism, although

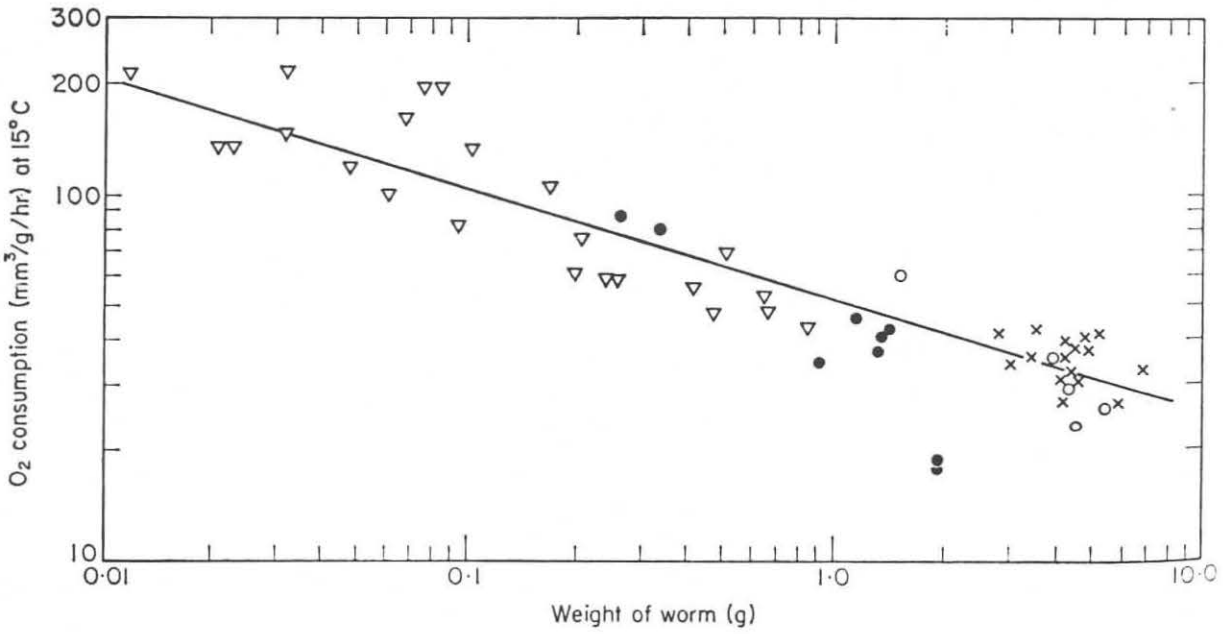

FIG. 33. Oxygen consumption by *L. terrestris* and *E. foetida* at 15° C. ▽, *E. foetida* (Kruger, 1952); ×, *L. terrestris* (Konopacki, 1907); •, *L. terrestris* (Davis and Slater, 1928); ○, *L. terrestris* (Raffy, 1930).

this is not explicitly stated by all the authors on whose work the figure is based. The respiration rates obtained take no account of motor activity such as burrowing or feeding, nor of any special metabolic conditions which may prevail during diapause.

(b) *Diurnal rhythm.* Fig. 34 illustrates, from the work of Ralph (1957), the existence of diurnal rhythms of oxygen consumption and activity in *L. terrestris*. The two apparently do not entirely coincide and Ralph suggested that earthworms may incur oxygen debts during periods of high activity.

(c) *Oxygen tension.* Certain species undoubtedly occupy habitats with very low oxygen tensions, e.g. *Helodrilus oculatus* in lake muds and at the bottom of wells. Although it has never been directly demonstrated, *L. terrestris* may also encounter oxygen concentrations sufficiently low to have a marked effect

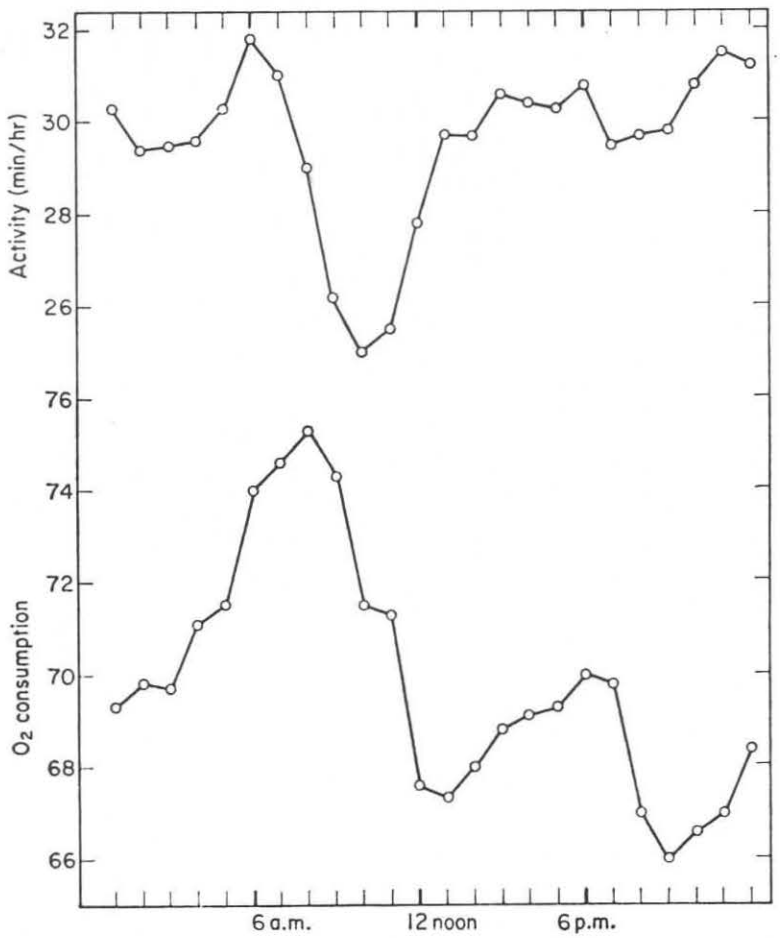

FIG. 34. Diurnal activity in *L. terrestris* (from Ralph, 1957). Units of oxygen consumption not given in original.

on oxygen consumption. In experiments continued for 2 hours at 10° C, Johnson (1942) found that when *L. terrestris* was kept in various concentrations of oxygen in nitrogen its oxygen consumption fell when the concentration of O_2 was decreased to 10% (partial pressure 76 mm Hg) and below. In 10% O_2 and in 5% O_2, oxygen consumption was about 93% and 47% of what it was at atmospheric concentration (20%). There appear to have been few studies in temperate regions of the composition of the soil atmosphere at the depths to which *L. terrestris* burrows, but the data of Boynton and Compton (1944) for a silty clay soil from an apple orchard at Cornell show oxygen

concentrations below 10% for about 11 weeks in the year at a depth of 3 ft and for 6 months of the year at a depth of 5 ft. Concentrations below 5% occurred for about 11 days and 4 months respectively at 3 and 5 ft (Fig. 35). It has been suggested that low oxygen tensions are responsible for earthworms leaving their burrows after heavy rain (Merker, 1928), but the evidence is inconclusive.

(*d*) *Carbon dioxide concentration.* It is generally believed that carbon dioxide concentrations in the soil do not affect respiration greatly. *Eisenia foetida* shows no behavioural response to concentrations up to 25% by volume (Shiraishi, 1954), and according to Stephenson (1930) the presence of CO_2 up to a proportion of 50% has only a slight and reversible effect on

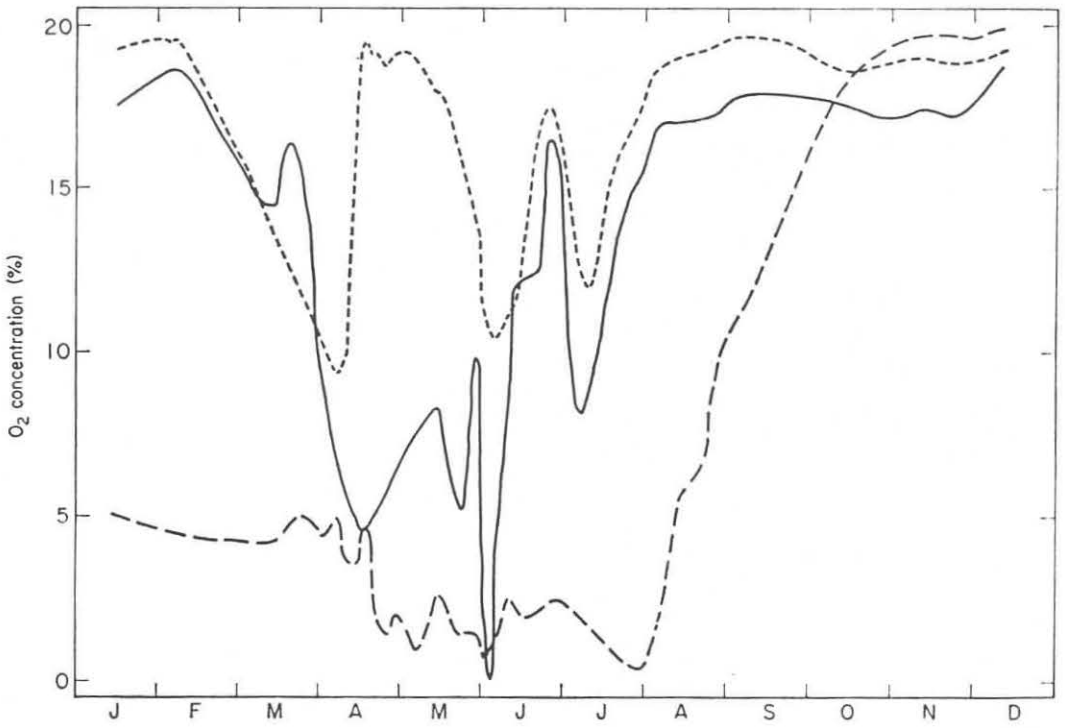

FIG. 35. The oxygen content of the soil at 3 depths of a silty clay apple orchard (adapted from Boynton and Compton, 1944). — — —, 5 ft; · · · · · ·, 7 ft; ————, 3 ft.

worms. Extreme limits of CO_2 concentration in soils quoted by Russell (1950) range between 0·01 and 11·5%.

(e) *Exposure to light.* The respiratory rate of *L. terrestris* is affected by exposure to light. Davis and Slater (1928) found that the rate was doubled in bright light and Johnson (1942) recorded a 30% increase in the rate of oxygen consumption when worms were first exposed to darkness and then to diffuse daylight. This may be significant in surface feeding species.

(f) *Ambient temperature.* The rate of earthworm respiration is greatly affected by the ambient temperature, and this is likely to be one of the most important factors affecting earthworm metabolism under field conditions.

The rate of pulsation of the dorsal blood vessel and the pseudohearts varies according to temperature (Rogers and Lewis, 1914) as do the dissociation curves of earthworm haemoglobins (Haughton, Kerkut and Munday, 1958). The respiration rate rises with increasing temperature. In poikilotherms generally the magnitude of the temperature effect, described by the Arrhenius constant, μ, has a value of 11,500 calories for a wide variety of respiratory processes (Prosser *et al.*, 1950). From experiments done at temperatures ranging from 9 to 27° C, a μ value of 11,040 ± calories has been found for *L. terrestris* (Pomerat and Zarrow, 1936), so the relationship between temperature and respiratory rate in earthworms appears to be similar to that reported for other poikilothermous animals.

However, the effect of temperature on respiration may be expected to vary seasonally as a result of acclimatization. In the tropical earthworm, *Megascolex mauritii*, the rate of oxygen consumption for winter animals at 20° C, determined in January 1960, was greater than that for summer animals, determined in June 1960, by about one-third in large specimens to four times in small specimens (Saroja, 1961). Attempts to induce respiratory acclimatization experimentally in *E. foetida* (Kirberger, 1953) have been inconclusive, but there seems no reason to suppose that acclimatization is less significant in the ecology of temperate than in tropical earthworms.

(g) *Body size.* In the Lumbricidae, as in other groups, the respiratory rate per unit weight is higher for small specimens of a given species than for large specimens. This is well illustrated by Gromadska's (1962) data for *L. castaneus* and Krüger's (1952) data for *E. foetida* and is consistent with Konopacki's (1907), Davis and Slater's (1928) and Raffy's (1930) observations on *L. terrestris* (Fig. 33). Müller (1943) found no such relationship for *L. terrestris* but as the individual weights of the specimens used in her experiments are not stated, the data are difficult to interpret. It will be seen from Fig. 33 that the respiration rates of *L. terrestris* and *E. foetida* are similar for animals of the same size. *A. caliginosa* has a lower metabolic rate, half grown worms of mean weight 0·5 g consuming 75 µl./hr per gram fresh weight at 15° C (Barley and Jennings, 1959) in contrast with about 125 µl./hr per g by *E. foetida* at this weight and temperature.

Although these respiratory studies were carried out at different temperatures by a variety of workers using different techniques, the results are reasonably consistent. They also agree with Needham's (1957) excretion data in showing that *A. caliginosa* has a relatively low metabolic rate, and they suggest that the difference in total nitrogen output of *L. terrestris* and *E. foetida* may largely result from their different body sizes.

2. *Computation of carbon combustion by field populations*

The direct contribution made by earthworms to decay can be estimated from respirometer data. Such an estimate has been made for an Australian population of *A. caliginosa* by K. P. Barley (1964) from whose work the following paragraph is quoted.

"At 15° C the oxygen consumption of worms of bodyweight 0·2 g—a mean commonly found for field populations—is in the region of 100 μl. per g bodyweight per hr. The metabolic rate in the field is likely to be less than that measured in a respirometer, and a generous estimate is 50 μl per g per hr. For a population of 80 g/m² active for 150 days this rate corresponds to an oxygen consumption of 14 l./m²/yr. This figure may be compared with the total amount of oxygen consumed in decay each year on pasture land at Adelaide. A pasture producing 7,000 lb dry matter per acre (8,000 kg/hectare) returns the following amounts (8,000 lb/acre) of material to the soil: herbage litter 3·5 (Carter 1962); dung, 1·4 (Hutchinson and Porter 1958); dead roots, 1·4 (root: shoot ratio 1:5); total 6,300 lb/acre. The increase in residual organic matter per year, corresponding to an addition of 0·004% nitrogen in the top 6 in. of soil, is 1,600 lb/acre. The amount of material oxidised is 6,300–1,600 = 4,700 lb/acre ≃ 500 g/m². This is nearly equivalent to the weight of oxygen consumed or to a volume of $500/32 \times 22{\cdot}4 = 350$ l./m²/yr. Thus, neglecting other members of the food chain, earthworms bring about only a small fraction, of the order of 4% of the total decay."

A similar conclusion is reached when Fig. 33 is used to estimate the oxygen consumption of woodland populations of *L. terrestris*. In the study of *L. terrestris* in Merlewood Lodge Wood and Heaning Wood every worm collected was weighed individually. The monthly biomass estimates (Fig. 32) were then apportioned to weight groups differing by half gram units and a mean oxygen consumption rate for each group was obtained from Fig. 33. After summing the products of this rate and the biomass for each size group the total was adjusted to the prevailing soil temperature using the Krogh curve. Estimates of the annual oxygen consumption by the two populations obtained by summing the monthly estimates are given in Table XIX, together with closely similar results calculated by a simpler method.

At the mean soil temperature for the year's sampling in Merlewood Lodge Wood, 22·87 l./m² of oxygen is equivalent to a carbon consumption of 118·6 kg/ha. A reasonable estimate of the litter fall and composition on this site would be about 3,000 kg/ha dry weight and, on an ash free basis, a carbon content of about 50% and a C:N ratio of about 38. The carbon combustion by the *L. terrestris* population might therefore amount to about 8% of the total, which would reduce the C:N ratio to a little below 35. Only material with a C:N ratio of 20 or lower can directly provide mineral nitrogen, so that the effects of the earthworm's respiratory metabolism may be less in this respect than those of other groups such as nematodes with a lower biomass but a higher metabolic rate.

The foregoing calculation is based on the respiratory rate of inactive animals, so the true consumption of carbon by the field population is likely to be higher than the 8% indicated. There is little direct evidence of how the metabolic rates of active and inactive worms compare nor of the duration of activity in the field. Ralph's (1957) oxygen consumption data for periodically active *L. terrestris* (Fig. 34) show a maximum consumption about 13% higher than the minimum consumption, and Raffy (1930) found the consumption of

L. terrestris exposed to light at 16° C between 31% and 64% higher than at the same temperature in the dark. As exposure to light produces strong negative phototaxic activity, it seems unlikely that the difference between resting metabolism and active metabolism in the field would be greater than observed in this experiment. The amount of carbon respired by the population may therefore be as much as 12% of that present in the litter fall, but is unlikely to be more.

TABLE XIX

Annual Oxygen Consumption of *L. terrestris* populations

	Merlewood Lodge Wood Jan.–Dec. 1960	Heaning Wood May 1962–April 1963
Total number of *L. terrestris* taken by formaldehyde sampling	2,837	13,974
Total weight of *L. terrestris* taken by formaldehyde sampling	7,735 g	30,026 g
Mean weight/worm	2·7 g	2·2 g
O_2 consumption at 15° C at mean weight/worm from Fig. 33	36 μl./g per hr	39 μl./g per hr
Mean soil temperature for year	9.0° C	8·2° C
Krogh correction factor	0·545	0·491
O_2 consumption at mean soil temperature at mean weight/worm	19·6 μl./g per hr	19·1 μl./g per hr
Mean of monthly biomass estimates	121·4 g/m²	133·0 g/m²
Estimated annual O_2 consumption by population	22·52 l./m²	22·25 l./m²
Estimate obtained as described in text	22·87 l./m²	22·77 l./m²

3. *Comparison of population metabolism of earthworms and other groups*

Mellanby (1960) pointed out that Hansen's famous statement that, "the weight of earthworms in pasture land may exceed the weight of stock grazing on it" may be misleading if taken as more than a picturesque analogy. Because the metabolic rate of earthworms is less than that of mammals and may be decreased by aestivation and cold torpor, Mellanby concluded that an earthworm biomass of 1,000 lb/acre would be "biologically equivalent" not to a 1,000 lb bullock but to a 10 lb hare. A possible corollary might be that if the energy demand on the ecosystem by earthworms is only about 1% of that of bullocks for the maintenance of the same biomass, the attention of agronomists might be directed to the possibilities of cropping earthworms as a source of animal protein. However, the concept of "biological equivalence" is generally used by soil zoologists to mean that the contribution of different animals to the transformation of plant residues in the soil may be

estimated by comparing their oxygen consumption. Macfadyen (1963), for example, states that, "the population which exploits the greatest quantity of stored energy is contributing most to the rapid liberation of nutrient substances."

The estimates of the oxygen consumption of the *L. terrestris* populations of Merlewood Lodge Wood and Heaning Wood (p. 311) enable provisional comparisons with livestock and other soil groups to be made.

On the assumptions that:

(1) an "average" pasture carries about 500 kg of stock per hectare;
(2) the basal oxygen consumption of a bullock is 132 cc/kg per hr (Brody, 1945);
(3) the energy required for normal activity by stock is about twice that of its basal metabolism (Brody, 1945);

the annual oxygen consumption of dairy stock may be estimated as of the order of 115 l./m^2. The estimates of the annual oxygen uptake by the *L. terrestris* populations of Merlewood Lodge Wood and Heaning Wood, both about 23 l./m^2, suggest that the energy loss in agricultural grassland may indeed be greater through the stock than through the earthworms, though by a factor nearer 5 than 100.

Recent estimates of the oxygen consumption of field populations of oribatid mites (Berthet, 1963) and Enchytraeidae (O'Connor, 1963) are available. Despite obvious differences from the Lumbricidae in behaviour, all three groups appear to feed on a mixed diet of plant litter, humic material and micro-organisms, so that there is some justification for using the oxygen consumption of these groups for comparing their contribution to soil metabolism. Berthet calculated that the adult oribatids of a broad-leaved forest consumed about 4·5 l.O_2/m^2 per annum, and considered this would be trebled if nymphs had been included in the estimate. Even so, the annual respiration of oribatid populations appears to be less than that of the earthworm populations of woodland mull, their higher metabolic rate failing to compensate for their small biomass. O'Connor (1963) has estimated that the enchytraeid population of a conifer plantation in Wales with a mean biomass of 10·8 g/m^2 consumed approximately 31 l. O_2/m^2 per annum, about a third more than the Lake District *L. terrestris* populations weighing about 12 times as much. O'Connor calculated that the energy of respiration for the enchytraeids was about 150 kcal./m^2 per annum. For the *L. terrestris* populations it would be about 110 kcal./m^2 per annum (R.Q.=0·78, av. of 18 determinations by Konopacki, 1907) or about 10 and 8% respectively of the energy content of an annual litter fall of 3,000 kg/ha. The importance of other groups of soil animals may therefore exceed that of the Lumbricidae in their direct contribution to soil metabolism. However, earthworms are unique amongst soil animals in the extent to which they bury organic debris, mix organic and inorganic matter in their excreta and modify the structure of the soil with their burrow systems, and their direct effect in mobilizing nutrient substances may be insignificant compared with the catalytic effects of their

activity on microbial metabolism. It must be stressed again that the estimates given of rates of nitrogen, carbon and energy flow through earthworm populations involve many assumptions and are to be regarded as imaginative speculations aimed at exploring the implications of the little knowledge we have.

VII. THE INFLUENCE OF EARTHWORMS ON SOIL MICRO-ORGANISMS

A. Changes in Microbial Populations in the Earthworm Gut and Faeces

Publications on the influence of earthworms on the microflora of the soil contain many conflicting observations, but it is now generally agreed that the earthworm gut contains essentially the same kinds of organisms as are present in the soil in which the worms are living. Bassalik (1913) isolated more than 50 species of bacteria from the alimentary canal of *Lumbricus terrestris* and found none which was not present in the soil from which the worms came. More recently, Parle (1963b) examined the gut of 3 species of earthworm and found no micro-organisms which are not common in soil or plant remains. In particular, he investigated the possibility that the cellulase and chitinase present in the alimentary canal of earthworms might be secreted by special symbiotic micro-organisms such as occur in molluscs. He concluded that although some cellulolitic and chitinolitic activity was attributable to soil organisms present in the gut contents, the enzymes were secreted mainly by the earthworms themselves. It seems likely therefore that earthworms possess no indigenous gut microflora.

The extent to which earthworms digest micro-organisms is, however, less certain. The crops, gizzards and intestines of earthworms have been examined for large micro-organisms by Aichberger (1914), who found there very few organisms not possessing firm outer coats and no live yeasts, diatoms, desmids, blue-green algae or rhizopods. Moreover, Protozoa appear to form an essential constituent of the diet of at least one species of earthworm, the dung hill and compost inhabiting *E. foetida*. It is apparently unable to grow to sexual maturity in the absence of the motile Protozoa normally so abundant in its environment (Miles, 1963). There are only two records of bacteria being killed out after ingestion by earthworms and both were non-autochthonous forms, *Serratia marcessens* (Day, 1950) and *Escheria coli* (Brüsewitz, 1959), introduced to the soil by inoculation. Day (1950) also found that *Bacillus cereus* var. *mycoides*, in a heavily inoculated soil, decreased in numbers after ingestion by *L. terrestris*, but persisted at low densities in a way suggesting considerable destruction of vegetative cells but not of spores. In general, however, in uninoculated soils, numbers of yeasts and fungi are little changed in passage through the earthworm gut and bacteria and actinomycetes increase exponentially from fore-gut to hind-gut (Table XX).

Earthworm faeces emerge as a saturated paste, poorly aerated but rich in ammonia and partially digested organic matter. The ensuing changes in

microbial numbers were first recorded by Stöckli (1928). He found that the total cell count doubled in the first week after the casts were formed and remained at about this level, though with considerable fluctuation, for a further 3 weeks (Fig. 36). Parle (1963a) found no consistent changes in num-

TABLE XX
Numbers of actinomycetes and bacteria in different sections of *L. terrestris* intestine* (from Parle, 1959)

	Fore gut ($\times 10^6$)	Mid gut ($\times 10^6$)	Hind gut ($\times 10^6$)
Actinomycetes	26	358	15,000
Bacteria	475	32,900	440,700

* Means of 5 samples counted by double dilution technique.

bers of actinomycetes or bacteria in ageing casts but yeasts increased and fungi, present almost entirely as spores in the gut, started to germinate in the casts and hyphae were most abundant in casts 15 days old (Fig. 25). These changes in numbers of micro-organisms are in marked contrast with the

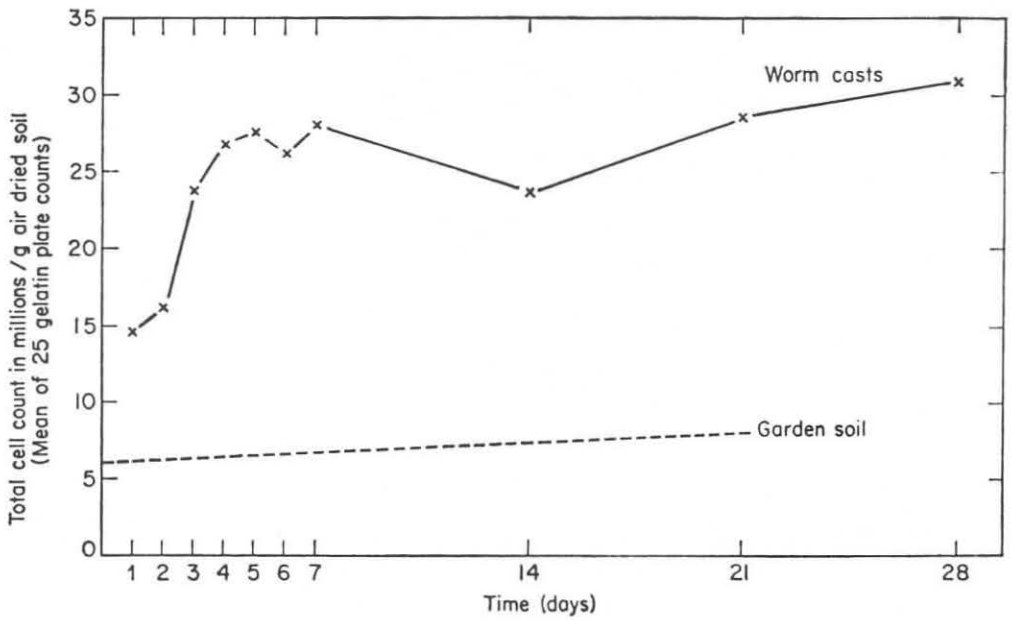

FIG. 36. Total cell counts from earthworm casts of different ages, and garden soils (from Stöckli, 1928).

course of microbial activity shown by the oxygen consumption of casts of increasing age, which declines consistently from the time when the cast material is excreted (Parle, 1963a). When glucose or cellulose is added to casts of different age total oxygen uptake increases but the older casts continue

to respire at a lower rate than those produced more recently (Fig. 37). The effect therefore does not seem to arise from the exhaustion of energy supplies or from a decline in the microbial population—it occurs when this is either increasing or stationary—but because an increasing proportion of the population forms resting stages as the casts age. Ruschmann (1953) reported that *Nocardia polychromogenes*, *Actinomyces* spp. and *Streptomyces coelicolor* isolated from worm casts or gut contents are particularly antagonistic to aerobic spore-forming bacteria, and the decline in respiratory exchange in the casts may result from an antibiotic effect of their dense populations of actinomycetes.

Many investigations have shown that the microbial population of casts is generally higher than that of surrounding soil, but it is rarely possible to

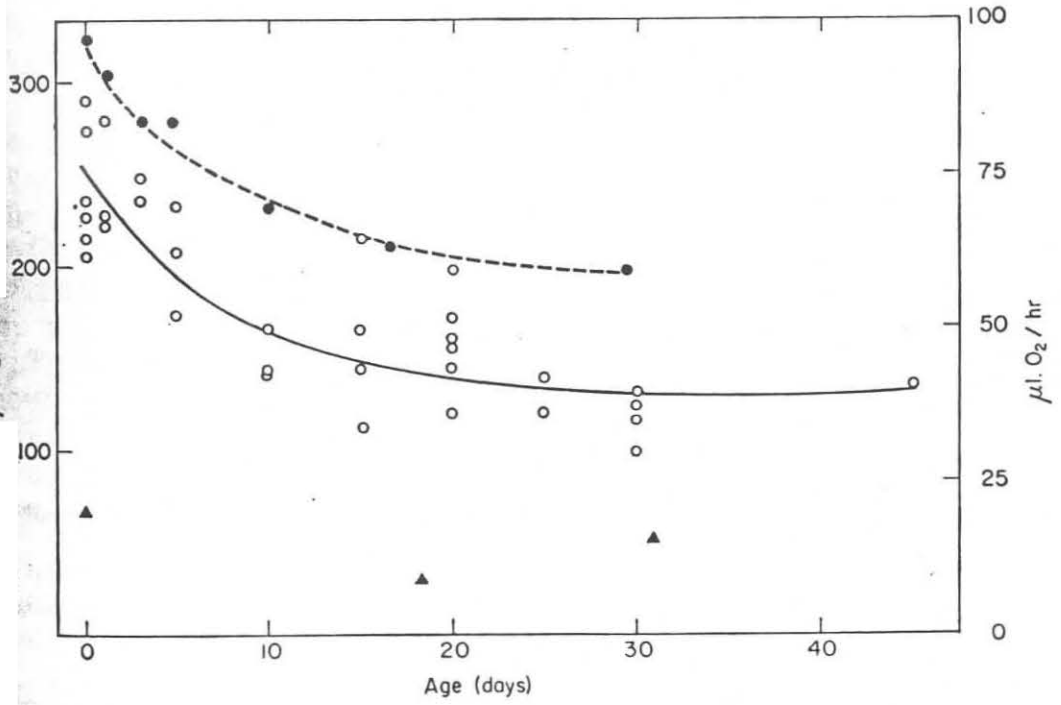

FIG. 37. Left, oxygen uptake in 8 hr by cast material at different ages. ○, cast; ▲, soil. Right, oxygen uptake in 1 hr by cast material of different ages in the presence of excess glucose (●) (from Parle, 1963a).

distinguish how far this arises from selective feeding on materials forming a substrate for microbial activity and how far it arises from changes brought about in the earthworm's intestine. Undoubtedly the size of the increase in the microflora in earthworm faeces depends largely on the amount and type of plant material in the soil ingested (Fig. 38b) but, as has already been shown, the numbers of bacteria and actinomycetes in the ingested material increase considerably in the gut. The size of the increase under field conditions may be assessed from Parle's results. He estimated that the bacteria and actinomycetes were up to 1,000 times more numerous in the gut than in the surrounding

soil, and that the oxygen uptake by cast material was still considerably higher than that of the soil after 50 days.

Three workers found fewer or the same number of micro-organisms in casts as in soil, but these apparently anomalous results may be accounted for by the experimental procedures used. All worked with earthworms in containers of prepared soil. Day (1950) found no consistent difference between the bacterial numbers in firmly tamped soil and fresh excreta produced by specimens of *L. terrestris* as they burrowed into it. Under these conditions ingested soil passes through the gut in 11 to 12 hours (Parle, 1963b), which is about twice the rate for worms feeding normally and probably too quick for the bacteria to multiply detectably. Jeanson-Luusinang (1963) also found no

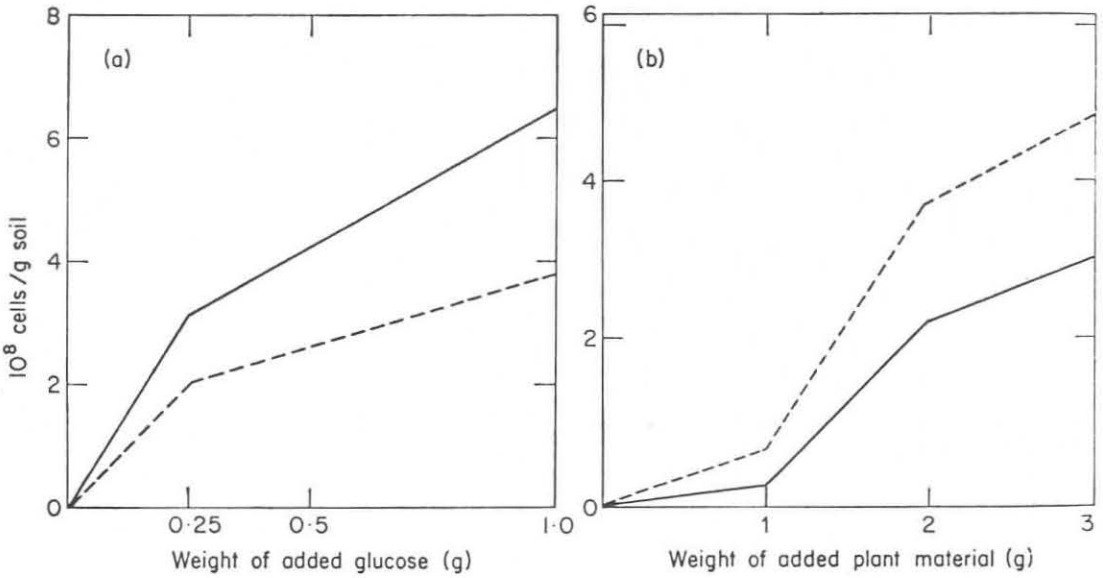

FIG. 38. Microbial cell content of faeces produced by *E. foetida* when kept in subsoil with different amounts of glucose (a) and dried, ground plant material (b). ————, Subsoil; — — —, casts (from Brüsewitz, 1959).

significant difference in microbial numbers between soil and excreta of *L. terrestris* but in this experiment milled lucerne was mixed with the soil, which was kept at field capacity and maintained for 1 month at 18–22°C. Lucerne is a readily decomposed, nitrogen-rich energy source and as it was milled and dispersed in the soil under virtually optimal conditions of moisture, aeration and temperature it is scarcely surprising that ingestion of the medium by earthworms had no further effect on microbial abundance. In the third example glucose was added to the worm cultures and cell counts were lower from casts than from soil (Brüsewitz, 1959) (Fig. 38a). Again with a rich energy source already available in the soil, the increased availability of organic supplies in the gut would be of less significance. Indeed, competitive utilization of the glucose combined with some digestion of the micro-organisms may have contributed to the observed decrease in the population in the ingested soil.

Finally, in pot experiments with various earthworm species, Went (1963) obtained bacterial counts from earthworm faeces intermediate between the low density in the clay soil in which the worms were kept and the high density in alder leaves on which they fed. Alder leaves have an exceptionally high nitrogen content and decompose so fast that earthworm activity would be unlikely to accelerate it appreciably. Although bacterial numbers were higher in rotting alder leaves than in the mixture of leaf and mineral matter comprising the earthworm faeces, the results do not preclude the conclusion that ingestion by earthworms increases the rate of decomposition of materials more resistant to microbial attack.

B. Stimulation of Microbial Decomposition by Earthworm Activity

It is well established (Tenney and Waksman, 1929; Harmsen and van Schreven, 1955) that simple nitrogen compounds added to nitrogen-poor organic materials are readily incorporated into microbial protein and accelerate the organic materials' decomposition. It would be expected, therefore, that in incorporating plant litter with soil enriched with their nitrogenous excreta, earthworms not only decompose material themselves but stimulate other decomposers. The effect is illustrated in an experiment (Barley and Jennings, 1959) in which grass and clover litter with a nitrogen content of 2·5% and dung pellets were left to decay in cultures of soil with and without young specimens of *A. caliginosa*. The concentration of worms in the cultures, 3 g/kg, was within the range encountered in the field. The cultures were kept moist, well aerated and at 15° C for a period of 45 days, during which their oxygen consumption was recorded and also the rate of ammonium and nitrate accumulation for a further 5 days. The oxygen consumption of the worms alone at 15° C was estimated in a separate experiment (Table XXI).

TABLE XXI

Influence of *A. caliginosa* on the decomposition of herbage litter and dung (from Barley and Jennings, 1959)

Treatment	Oxygen consumption from 15 to 45 days (μl./g of medium)	Log value	Nitrate + ammonium N accumulated in 50 days p.p.m.	Log value
With worms	2600	3·39	129	2·10
Without worms	2190	3·32	105	2·01
Min. sig. diff. ($P=0·01$)	—	0·05	—	0·09

The cultures with worms consumed 410 μl.O_2/g of medium more than those without worms, and it was estimated that 200 μl. of this was consumed by the worms themselves. Table XXI shows that worms increased the rate of decomposition by about one-fifth to one-sixth, due, about equally, to their own

action as decomposers and to stimulating other decomposing organisms. The temperature, moisture, aeration and supply of relatively easily decomposed organic matter was such as to favour microbial activity even without earthworms, so their activity probably modified the microbial environment less than it would under field conditions.

Composting techniques for vineyard residues also show how earthworms stimulate microbial decomposition. Anstett (1951) incubated grape husks at 25 to 30° C in pots, some of which he inoculated with *E. foetida*. After 5 months the microbial population was 4 to 5 times greater in the inoculated pots. Decomposition of the husks was measured by loss on ignition, which was 75% in the inoculated pots and 86% in the controls at the end of the experiments. The additional decomposition in the presence of *E. foetida* appeared to result mainly from the increased population of micro-organisms, since the

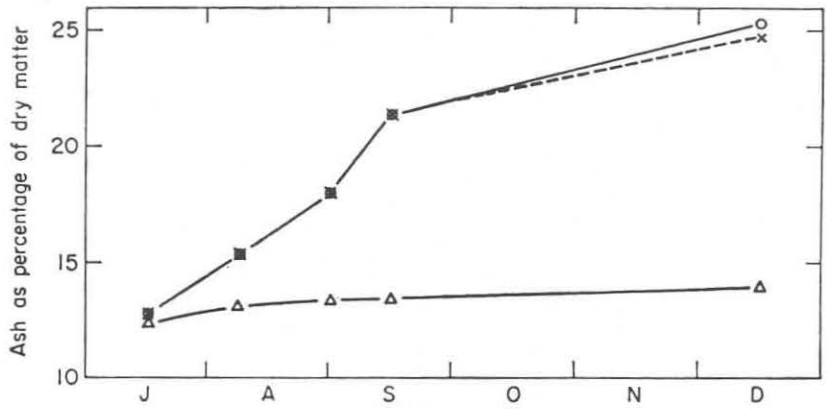

FIG. 39. Loss on ignition of decomposing grape husks in the presence and absence of *Eisenia foetida* (data from Anstett, 1951). △, without worms; ○, with worms; ×, with worms to September 1st, then without.

losses on ignition were the same from pots which contained worms throughout the experiment and from pots from which they were removed after 6 weeks (Fig. 39).

The effect of earthworms on the decomposition of more resistant organic residues, e.g. forest litter, has been little studied but clearly should not be judged by the oxygen consumption and/or excretory output of the worms themselves. On present evidence, conditioning plant remains for microbial decomposition seems to be the most important action of Lumbricidae in the ecosystem.

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